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The habitats of the Western Australian soldier crab *Mictyris occidentalis* Unno 2008 (Brachyura: Mictyridae) across its biogeographical range

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Abstract

The habitats of the Western Australian soldier crab, *Mictyris occidentalis* Unno 2008, were examined across its entire biogeographic range. The species transcends a range of environments from tropical, semi-arid to sub-tropical, arid climates, microtidal, macrotidal, to extremely macrotidal ranges, in different regional coastal sectors, and in various large-scale coastal geomorphic units such as barred lagoons, semi-protected beach/dune shores, and tidal creeks and lagoons in deltaic complexes and limestone barrier coasts. Locally, the species inhabits a variety of smaller-scale coastal geomorphic units (or habitats), including point bars, sloping beaches, shore-parallel shoals, tidal-delta shoals, tidal-creek shoals, tidal-creek banks, sand flats at low neap-tidal levels to mean sea level, mid- to high-tidal sand flats, and in discrete areas it may occupy sand flats up to the level of high-water spring tide and near the highest astronomical tide. It also inhabits sand flats behind mangroves, and locally may occur on sand flats within mangrove vegetation. The most significant factors determining soldier crab habitats are relatively stable, low to moderate wave-energy environments (so that their subsurface air cavities are not continually disrupted), exposure during low tides so that they can swarm and carry out shallow horizontal tunnelling without tunnel collapse, and sandy substrates comprising fine to medium sand (125 μm to 250 μm modal grain size) that can be pelletised, with generally < 8% mud content, 0.4–3.4% organic carbon content, a water table generally 10–15 (–20) cm below the surface at low tide, sand damp enough during low tide so that the surface can be tunnelled without collapsing, and/or pelletised, *i.e.*, a pellicular water content generally > 16%, groundwater and pellicular water that is less than hypersaline (groundwater salinity of 31–45 ppt, and a pellicular water salinity of 27–44 ppt) and, if located above MSL, a general absence of mangrove or salt marsh roots that would otherwise hinder horizontal tunnelling. Above levels of mean low water neap tide, tidal level is not a major factor – though mostly found in low-tidal environments and above the level of mean low-water neap tide, if there are appropriate damp surfaces and dilution of hypersaline groundwater and pellicular waters by marine water or fresh-water discharge, soldier crabs can inhabit sandy environments from mean low-water neap tide to above mean high-water spring tide, even to levels near the highest astronomical tide. Local stratigraphy under the tidal-flat and coastal zones can determine soldier crab habitat in that it can influence delivery of seawater or fresh water to maintain the habitat moisture levels and salinity. Microtopography within the habitat is important for determining the distribution of the crab at finer scales by providing suitable moisture conditions for feeding, tunnelling and other ichnological constructions.

Keywords: *Mictyris occidentalis*, soldier crab, habitat, tidal flats, beaches, Western Australia

Introduction

The Western Australian soldier crab, *Mictyris occidentalis* Unno 2008 is endemic to the north-west of Western Australia and its biogeographic range extends over ~ 900 km of coastline (latitudinally) from One Arm Point at the northern end of the Dampier Peninsula to Monkey Mia, Shark Bay in the south (Unno 2008a; and Figures 1 and 2). However, soldier crab populations are not ubiquitous along the coastline but occur discretely in specific zones or niches in intertidal habitats [the term niche is used here *sensu* Grinnell (1917) as a subdivision of the habitat, not as the ecological role of the organism]. Niche partitioning, or zonation of crab species across the intertidal environment, occurs as a biological response to local gradients occurring in biotic and abiotic environmental characteristics as a given species adapts to the conditions found in the niche existing at a particular location along the gradient (Hutchinson 1957; Dunson & Travis 1991).

This paper defines the biogeographic range of *Mictyris occidentalis*, describes the variety of habitats of the species across its entire biogeographic range, details the main abiotic features that characterise the local habitat of this species, and provides a general model for predicting the presence of soldier crab populations along suitable coasts. Since the soldier crab responds to a variety of interacting abiotic factors such as shore type, sediments, hydrology, salinity, and organic matter, amongst others,

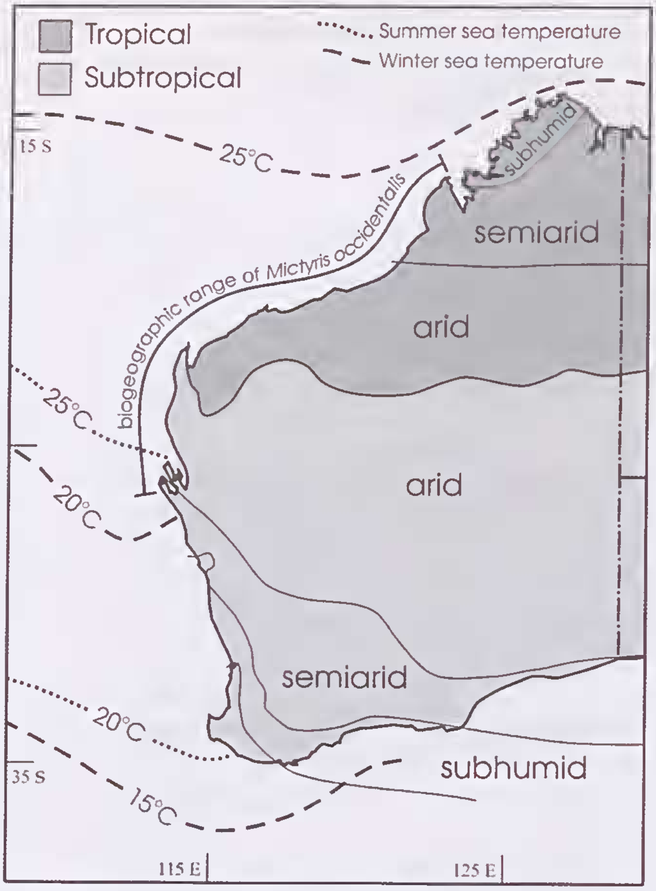


Figure 1. Map of Western Australia showing generalised climatic zones (after Gentilli 1972), surface sea temperatures (after Reynolds 1982), and biogeographic distribution of *Mictyris occidentalis*. Though the Leeuwin Current markedly complicates the surface sea temperatures along the Western Australian coast, the map by Reynolds (1982) provides a time-averaged pattern adequate for comparatively showing distribution of soldier crabs against sea temperatures.

there is some focus in providing background information on these features and how they operate and vary along the Western Australian north-west coast, as they have relevance to the development of the soldier crab habitat. While the scope of this study involves the investigation and description of selected abiotic factors within the habitat of the Western Australian soldier crab, biological factors which may determine or control its occurrence (such as competition by other benthic fauna, commensal organisms, or predators) are not considered. The effects of mangroves and sea couch are briefly considered.

Literature on habitat description for intertidal brachyurans, as well as *Mictyris* species outside of Western Australia, is reviewed to determine the extent that crab habitat descriptions have been carried out, and to assess the different habitat factors other authors have considered as significant in determining general crab abundance or distribution. These reviews provide information on and insights into, the abiotic determinants of crab occurrence in general, and soldier crab occurrence in particular in the intertidal environment, that are useful to investigate in this study.

This study of the habitats of a species of *Mictyris* across its subcontinental extent in Western Australia, systematically examining all habitats where it occurs, noting the types of habitat where it does not occur, and describing the characteristics of its habitat, is a world first for this approach and results for this genus.

There is a unique feature of the Western Australian soldier crab: worldwide, in the biogeographic region of the genus, it is the only species of *Mictyris* that occurs along an arid coast (Figure 1). The north-west coast of Australia, centred on the tropical arid Pilbara Coast, extending northwards to the tropical semi-arid Broome region, and southwards to the sub-tropical arid Shark Bay region, is the most arid coast in Australia, and one of a limited number of arid coasts globally (Semeniuk 1996). In contrast, all other species of *Mictyris* occur along humid coasts. The Australian context of species of *Mictyris* is particularly interesting in this regard in that three other recorded species of *Mictyris* occur in Australia, located along tropical humid coasts in Queensland, subtropical humid coasts in New South Wales, and temperate humid coasts in Tasmania. Thus, while the results pertaining to the Western Australian soldier crab may not be directly related to the other species of *Mictyris* in detail, it is the principles of its autoecology derived from this study that can be applied elsewhere.

Acronyms and terms

Acronyms for tidal levels used in this paper follow standard procedure: HAT = highest astronomical tide; MHWS = mean high water spring tide; MHWN = mean high water neap tide; MSL = mean sea level; MLWN = mean low-water neap tide; MLWS = mean low-water spring tide, LAT = lowest astronomical tide; AHD = Australian Height Datum. Tidal range terms are (following Semeniuk 2005, modified after Davis 1980): microtidal < 2 m; mesotidal 2–4 m; macrotidal 4–8 m; and extreme macrotidal > 8 m.

Most of the terms for coastal landforms, geomorphic units, sediments, ecological functioning and biology used throughout this paper are established in the literature. However, we have deviated from the use of a particular coastal term, "ridge-and-runnel", as explained below. In the literature, "ridge-and-runnel" generally refers to the system of asymmetrical ridges (sometimes referred to as "bars") that run parallel to the coast and are separated by shallow troughs (or runnels) 100–200 m wide. This topography is usually developed on mesotidal and macrotidal sandy shores (or beaches) by moderate wave energy acting on low, sloping shores. However, while used extensively in the literature, there generally is little definition or morphometrics, or imprecise use of the term ridge-and-runnel systems (though there are exceptions, *e.g.*, King 1972, Greenwood & Davis 1984; Nummedal *et al.* 1984; Short 1984; Reichmuth & Anthony 2002). Along the macrotidal north-western Australian coast, there are low-relief, broadly convex sand bodies, generally cross-sectionally symmetrical (< 50 cm relief but usually ~ 30 cm relief), forming as shore-parallel systems some 50–100 m wide and 100–200 m long, as two to four or five sets parallel to the shore, and separated by "troughs" (of similar lateral dimensions to the convex sand bodies or narrower) that usually drain free of water at low tide. These low-relief sand bodies are important as soldier crab habitats in the low-tidal zone. They could be referred to

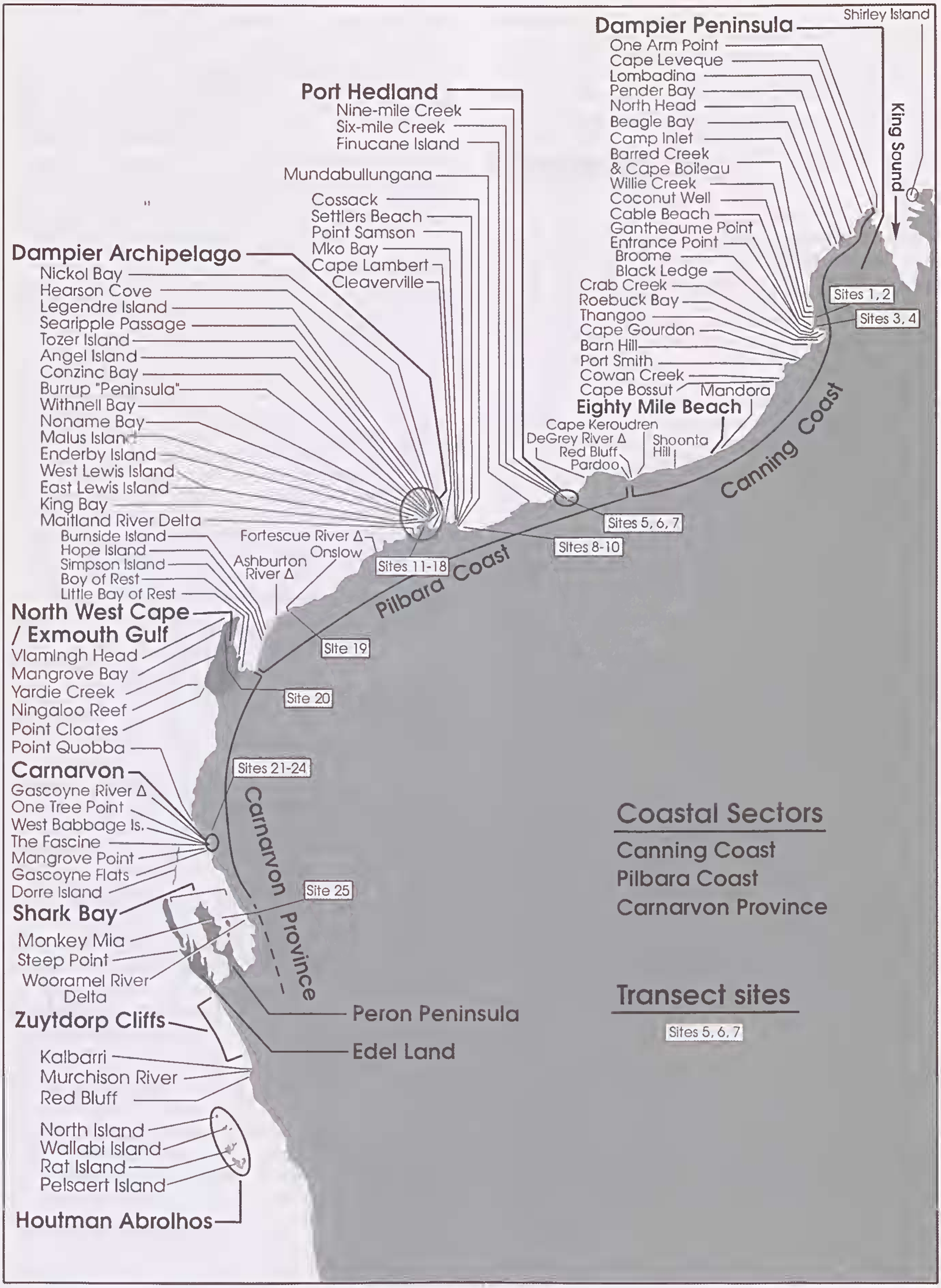


Figure 2. Geographic locations mentioned in text, and location of the twenty-five study (transect)sites.

as "ridge-and-runnel", however, what is described as such in the literature appears to be higher relief and more dynamic than those occurring along the shores of our study area. The convex sand body may also be termed a "bar" (*cf.*, Woodroffe 2002). We have preferred to use the term "shoal" instead of "ridge" or "bar" for the reason that the sand bodies generally are not of high enough relief to be described as ridges, and because the term "ridge" carries the implication of being long and narrow, or a crest, and is a term that does not encapsulate the notion of a low-relief, broadly convex sand body. The term "bar" carries the connotation of a discrete shape. The sand bodies in our study area vary from being discrete, isolated forms to mutually-merging sand bodies with an indefinite form, hence the term "bar" is not applicable to all. We have used the term "shoal" rather than "ridge" to refer to low mounds of sand that vary from being discrete to diffuse, and from being isolated to merging with adjoining shoals. In the latter situation they occur as part of what we term broadly as a shoal complex (and probably equivalent to some types and aspects of "ridge-and-runnel" systems). We use the term "bar" for discrete, isolated, sand bodies that stand with some relative relief (*e.g.*, > 30 cm) above the surrounding lower-relief tidal flat.

Review of habitat description for intertidal brachyurans other than *Mictyris* species

Few studies have focused on holistically describing habitats of intertidal brachyurans – there has been more of an emphasis on zonation of crabs across tidal environments. For instance, while zonation in crab species has been noted previously on: tidal flats (Wada 1983; Dittmann 2000), mangrove swamps (Warner 1969; Frith *et al.* 1976), rocky shores (Bennett & Pope 1953; Ingólfsson 2008), beaches (Dahl 1952; Janssen & Mulder 2005; Neves *et al.* 2007), and for particular taxa (Ono 1962; Crane 1975), which implies niche partitioning and abiotic gradients within the habitat, few studies present detailed description of habitats. That is, the zonation of the organisms is the focus, rather than the factors underlying the zonation or the habitat in which the zonation occurs. Exceptions include the work of Frusher *et al.* (1994) who studied the distribution of grapsid crabs in relation to sediment characteristics, salinity tolerance and osmoregulatory ability, and Janssen & Mulder (2005) who examined zonation on nine beaches on the Dutch coast in relation to macrobenthos (abundance, diversity and biomass), sediment (grain size, sorting and calcium carbonate content), slope, penetrability of the sediment, position of the anaerobic layer and the presence or absence of stable burrows of macrobenthic animals.

Where studies have been undertaken on habitats of brachyurans (and this is the case for the Ocypodidae group including the well-known genera *Uca, Dotilla, Scopimera* and *Ocypode*), they tend to focus on local habitat description at one geographic location, even if there is study of multiple sites and investigation of multiple habitat factors. For example, da Rosa & Borzone (2008) examined the spatial distribution of *Ocypode quadrata* with respect to abiotic habitat variables such as beach-face slope, grain size and sorting, sediment moisture content, water salinity, and seasons (temperature), at 13 estuarine sandy beaches within a radius of 30 km within the one estuary.

Uca species, in particular, have been widely studied in regard to the influence of abiotic environmental factors on the distribution of various species, with sediment grain size, sediment organic content, and tidal levels being the most significant factors, and salinity, mangrove distribution, microhabitat, and temperature being of secondary importance (Crane 1975; Frith & Frith 1977; 1978; Icely & Jones 1978; Frith & Bruenmeister 1980; Chakraborty & Choudhury 1985, 1992; Jaramillo & Lunecke 1988; Shin *et al.* 2004; Lim *et al.* 2005; Bezerra *et al.* 2006; Lim & Heng 2007; Liao *et al.* 2008). However, again, these studies have not addressed habitat characteristics, or habitat variability, across the entire biogeographic range of any given species.

Thus, generally, while there have been autoecological studies of crabs in specific localities to investigate abiotic ecological determinants and relationships, there have been no comparative studies of habitats across the entire biogeographical range of a given species for any intertidal crab taxa, as presented in this paper for *M. occidentalis*. This is an important autoecological consideration, because it is possible that as climatic and other regional factors change, the characteristics of habitat that determine occurrence, abundance, and population structure of a given species can vary in importance and influence across regional gradients. This matter, however, is outside the scope of this paper.

In relation to habitat features which are significant for benthic intertidal brachyurans (and other intertidal macrofauna), a range of factors has been considered by various authors, including grain size (Brown 1983; McLachlan 1996; Nel *et al.* 2001; Nanami *et al.* 2005), tidal elevation (Degraer *et al.* 2003), wave energy (McLachlan 1990a; McLachlan *et al.* 1993), and salinity (Barnes 1967; Ysebaert *et al.* 1998), amongst others. Most authors determined that a multiplicity of environmental factors influenced organisms and determined their habitats. Ravichandran *et al.* (2007), for instance, considered substrate type, water level, and mangrove distribution to be the most important factors affecting the distribution, zonation, and species diversity of crabs in mangrove environments. Otani *et al.* (2008), in a study of six tidal flats, found that assemblages of macrobenthos were determined by the physical characteristics of the sediment (grain size) and elevation. Jaramillo *et al.* (1993) determined that wave energy, sediment grain size and water content significantly affected intertidal zonation patterns of macroinfauna on Chilean sandy beaches. Sassa & Watabe (2008) examined the role of the physical process of suction in intertidal sediments in relation to the burrowing performance of the sand bubbler crab, *Scopimera globosa*, and concluded that geoenvironmental conditions significantly influence habitat selection by macroinfauna. Hartnoll (1973) and Flores *et al.* (2005) observed that sand-flat topography and shore level determined the density of *Dotilla fenestra* populations, while Gherardi & Russo (2001) found that drainage and substrate grade (grain size) determined burrow distribution in the same species. Honkoop *et al.* (2006), on the other hand, while commenting that 12 previous quantitative studies around the world determined that gradients in sediment grain size correlated with zonation in benthic assemblages on beaches and intertidal flats, found that assemblages did not correlate well with tidal level or zonation in grain size on intertidal flats at Eighty Mile Beach, Western Australia and attributed this result to either a greater impact on community structure by biotic factors rather than abiotic factors, or the disturbance effect of a recent cyclone.

Review of previous research specifically on soldier crabs, particularly with relevance to habitat descriptions

The soldier crab habitat has not been comprehensively described previously in the literature. Much of the research on soldier crabs has focused on discrete aspects of the soldier crab such as its physiology (Maitland & Maitland 1992), ontology (Cameron 1965; Fukuda 1990), reproduction (Nakasone & Akamine 1981; Shih & Chang 1991), population (Shih 1995; Dittmann 1998), behaviour such as feeding and swarming (Cameron 1966; Quinn 1983), and ecological interactions such as, for example, the effect of crab activities on meiofauna (Warwick *et al.* 1991; Dittman 1993). In other words, to date, there have been studies at specific locations to obtain specific autoecological information. There has been little information provided on abiotic habitat characteristics though occasionally there has been cursory mention of habitat setting (*e.g.*, sand tidal flat), and occasionally, mention of a median grain size or range of grain sizes for the substrate. Barnes (1967) examined the salinity tolerance of *Mictyris longicarpus* in water, under laboratory conditions only, not in the natural soldier crab habitat. Takeda (2005) investigated the behaviour (emergence *versus* non-emergence) on a tidal flat of male and female *M. brevidactylus* during the breeding period in relation to water and air temperatures, and water level of the daytime low tide.

Other research on soldier crabs with a specific focus on substrate properties (usually as an indicator of substrate alteration due to the activities of soldier crabs) includes the work of Sadao (2002, 2003) who examined the effect of bioturbation by *M. brevidactylus* (referred to as *M. longicarpus* var. *brevidactylus*), on substrate meiofauna, bacterial activity and nutrient concentrations. Webb & Eyre (2004) studied the effect of burrowing and grazing by *M. longicarpus* on sediment biogeochemistry including sediment irrigation rates, benthic metabolism (as measured by O_2 production), and N_2 and organic carbon fluxes. Only one study investigated the influence of the habitat on the soldier crabs themselves: Rossi & Chapman (2003) suggested that topographical variability (humps and depressions) and sediment "types" (sediment from humps or sediment from depressions, *i.e.*, the sediment "types" are topographic variations, not sedimentologic variations) are factors contributing to the spatial variability of the abundance and size of *M. longicarpus* on the tidal flat. Physical characteristics of the sediment "types", such as interstitial water content, grain size, organic carbon content, *etc.*, were not quantitatively described and the dimensions of the topographical variables (humps and depressions) were not provided.

All of the work on soldier crab habitats cited above was carried out at single localities and usually involved only one or two variables. Worldwide, there have been no comparisons of soldier crab habitats across an entire biogeographic range of any given species, nor even comparisons across a local area such as an estuarine system. As this paper shows, soldier crab habitat features at one location *cannot* be applied to all soldier crab habitats elsewhere, even for the one species, particularly if the species crosses a wide gradient in climate and tidal ranges at a subcontinental scale.

The most relevant determinants of soldier crab occurrence in the intertidal environment selected for investigation

Based on literature reviews, important environmental factors affecting intertidal crabs in general include microclimate (temperature of air, water and sediment, humidity), wave energy (which determines sediment stability and, in conjunction with topographic elevation, grain size), topographic elevation relative to the tide (which determines frequency of flooding), salinity (of ocean water, groundwater and pellicular water), sediment characteristics (grain size, composition), food availability, inter-specific competition, and predators. The response to interactions of all these environmental characters will determine the abundance, size classes, and behaviour of any given species.

In regards to the major environmental factors determining the soldier crab habitat, the high- to mid-tidal to upper low-tidal flat position of the *Mictyris* niche on the tidal flat would indicate that tidal level and its associated derivative factors of depth to water table at low tide, pellicular water content, and salinity may be determining factors for a range of brachyura. Wave energy in the environment would determine the stability of the substrate – an important factor impacting on the benthic soldier crabs which do not have permanent, deep burrows and occur predominately in the upper 15 cm of the substrate. In association with tidal elevation, wave energy would also determine the grain size of the substrate.

The organic content of the substrate would be significant, as soldier crabs are floatation feeders (Quinn 1983) which selectively extract organic material directly from the substrate. The composition of the sediment (quartz sand *versus* calcium carbonate sand) may have some effect on soldier crabs, in that it may control micro-hydrochemistry and the flora that inhabits the grain surface, and to some extent moisture retention (if particles have intra-granular porosity). The salinity of ocean, tidal creek or groundwater also could have some effect, the former because the salinity of ocean and tidal creek determines what is delivered to the tidal flat, and the latter because groundwater, through capillary rise, can influence the salinity of pellicular water. The amount of pellicular water surrounding the sand grains at low tide and its resultant salinity would be pertinent to in-dwelling fauna such as soldier crabs.

There was a range of other environmental variables such as oxygen content, pH, local air and water temperatures, and humidity which we did not investigate for a number of reasons. Air temperatures, shallow-water sea temperatures, and humidity in the soldier crab habitat fluctuated widely over the day in response to cloudiness, wind, and rain; we decided to use time-averaged values from the literature for these parameters as indicative of the regional setting in which the soldier crabs occurred. Further, air and sea temperatures, and humidity were unlikely to be major factors determining the limits of the habitat at a given site. That is, the limits of occurrence of a soldier crab habitat *within* a tidal embayment could not be determined by these parameters, since air temperature, sea temperature, and humidity would not vary greatly over the extent of the whole tidal embayment (itself composed of a myriad of habitats within which the soldier crab habitat was only a small part). At the local scale, the daily variation of temperatures and humidity were more likely to influence diurnal and semi-diurnal behaviour of the crab as shown by Kelemec (1979), who observed that there were fewer soldier crab emergences at lower air and sediment temperatures. Regional air and seawater temperatures, and humidity, which do vary over larger distances could have more of an effect on the regional distribution of *M. occidentalis*, potentially determining its biogeographic limits.

With regard to oxygen content, soldier crabs inhabited substrates that were anoxic to oxygenated, or that varied from being anoxic to oxygenated over several days, hence this did not appear to influence the crabs and thus was not included as a determining factor. In regards to the pH of pellicular water and groundwater, soldier crabs inhabited substrates where groundwater was alkaline to weakly acidic; this did not appear to influence the crabs so we did not include this as a determining factor (though whether there was an upper or lower limit in pH that determined soldier crab survival was not explored).

Methods

The objectives of the study were to define the biogeographic limit of *M. occidentalis*, and then to define the habitat characteristics of the species within that region. A variety of methods was used to achieve these objectives: 1. regional surveys; 2. site-specific studies along transects; 3. field description of the soldier crab habitat; 4. experimental work to define sediment preferences; 5. determining plant-root influence on soldier crab occurrence; 6. laboratory analyses; 7. assessing exposure/shelter for sandy coasts; 8. assessing tidal level and sediment style information; and 9. data analyses.

Regional surveys

To determine the limits of soldier crab occurrence biogeographically, the types of coasts that soldier crabs inhabit, and to identify sites for more detailed transect study, wide-ranging field surveys of soldier crab occurrences along the coast were carried out. This involved visiting some 316 sites to determine presence or absence of potential soldier crab habitats, and presence or absence of soldier crab populations therein (Appendix 1). Soldier crabs do not occur ubiquitously along the tropical sandy shores of Western Australia (unlike species of *Ocypode* that are generally widespread in the upper tidal to supratidal zones of tropical and subtropical beaches of Western Australia). There are specific habitat requirements for the soldier crab, and because they can occur in discrete and varied habitats where such requirements are met (*e.g.*, seepage line along a beach face, or pocket beaches along a rocky shore), a widespread reconnaissance was specifically undertaken to determine if soldier crab habitats and soldier crab populations could occur in local patches within stretches of rocky shores, cliffed shores, and sandy beaches in addition to their obviously preferred habitat of low tidal low-energy sand flats. This required investigation along extensive rocky shores and cliffed shores and sandy coasts to locate any local pocket beaches, and any extensive, low-gradient tidal sand flats seaward of sandy beaches.

The regional survey was undertaken in two stages by road where accessible, or by helicopter, and by boat: between 1980–1995 (VS) involving ~ 35 sites, and between 1996–2008 (JU & VS), involving ~ 270 sites. At a given site, the extent of the coastal type generally for 1–2 km to a either side of the site along the coast was noted, *i.e.*, whether it was laterally extensive (such as along cliffed or rocky shores, or beach/dune shores, or alternating rocky shores and pocket beaches), or whether it was laterally heterogeneous (*e.g.*, composed of sheltered embayments, pocket beaches, exposed tracts of coast, and cliffed rocky coasts). The information obtained from regional surveys was supplemented by examination of aerial photography, again, to assess the lateral extent of a given tract of coast. This was particularly important in coastal settings where there were extensive, relatively homogeneous coasts comprised of cliffed shores, or extensive and exposed beach/dune systems.

To determine the northern biogeographic limit of the species, there was focus on King Sound. For the southern limit of the species, there was a focus on the coastal tract from the Northwest Cape and Shark Bay regions (in semi-sheltered bays, sandy mouths of tidal creeks, areas protected from the prevailing regional waves, or sandy low tidal areas leeward of and around spits), to the region of Zuytdorp Cliffs, the limestone cliffs extending to the cliff coast of Kalbarri, and on the Murchison River estuary (four sites therein). Because the most southern occurrence of *M. occidentalis* was in the Monkey Mia area, special effort was made to more fully investigate potential habitats and possible soldier crab occurrence in the Shark Bay region to determine whether the species extended to other locations in that coastal system. This involved examining some 72 sites in the Shark Bay region. While open sandy coasts were investigated, there was also an effort to examine barrier spit shores (because they provided some degree of wave shelter to leeward) and tidal flats that exhibited shoal and depression morphology. In the barrier spit settings, seaward and leeward environments were examined.

Also, even though the islands of the Houtman Abrolhos occur much further south than Shark Bay, and effectively outside of the known biogeographic range of *M. occidentalis*, because of the complication of the Leeuwin Current delivering warm tropical water to offshore areas to the south into the Houtman Abrolhos (Pearce 1997), and hence a possibility that larvae of the species could be regularly delivered to this reef-and-limestone island complex, or that there could be resident outlier self-sustaining soldier crab populations there, a dedicated survey of the island reef complex was undertaken. A low-altitude aerial survey of the Houtman Abrolhos showed its shores to be dominated by coral limestone cliffs, coral limestone shore platforms, coral gravel shores, and moderately steep, high-energy beaches, all highly unlikely as soldier crab habitats. Locally, there were sandy coves, sandy embayments, and tidal creeks, often fringed by mangrove along the upper tidal zone, and all with potential to be soldier crab habitats. The on-ground survey of Houtman Abrolhos involved twenty-four sites of these most likely soldier crab habitats.

A survey on the mainland coast to the east directly opposite the Houtman Abrolhos in the Geraldton-Oakajee area also was undertaken for the same reason: to assess the potential for soldier crab habitats, or whether there were outliers of soldier crab populations on any of the tidal sand flats.

At a given site, where there was suitable habitat (*viz.*, tidally-exposed sand deposits), soldier crab presence/absence was determined during low tide, in the first instance, by the occurrence or absence of their ichnological products (*viz.*, single pustules, pustular structures, rosettes, and exit holes; see Unno & Semeniuk 2008), and by the occurrence of surface-swarming crabs, and in the second instance, if ichnological products and crabs were not evident on the surface, by extracting and sieving 10 box cores (Unno 2008b) from appropriate habitat surfaces.

Information from the regional surveys on the occurrence of the soldier crab was supplemented by examining locality records for the species in the Western Australian Museum. Both types of information (the Western Australian Museum records and our survey results) provided an indication of the widespread nature of the soldier crab along the tropical to subtropical coast of Western Australia, though in discrete locations. From there, specific sites were selected for more detailed study.

Site-specific studies along transects

Soldier crab populations at twenty-five transect sites in seven major localities latitudinally, from Coconut Well, the northernmost site (18 km north of Broome) to the Monkey Mia area, the southernmost site, located in Shark Bay were sampled in July 2004 for detailed characterisation of their habitat (Table 1; and Figure 2). Latitude and longitude co-ordinates for each site were taken by Magellan GPS in the WGS84 system. Selection of the sites was based on ensuring a diversity of habitats, some degree of replication of habitats at least in different climate zones, accessibility of the site, and reasonable proximity to a standard port where information on tidal levels and tidal predictions was available. Aerial photographs and PanAIRama® images used in the site descriptions were obtained from the Department of Land Information (Landgate), Perth, Western Australia.

The large number of transect sites ensured that we sampled the diversity of the habitats and niches that the soldier crab occupied, documented its occurrence across nearly its full biogeographic distribution, and replicated some of the habitats in different climate zones and in different coastal settings. Traditionally, biologists studying *Mictyris* (and other species of Brachyura) have focused on dense populations with readily collectable data to describe the autoecology of a given species, or to explore some ecological principle. There has been less

Table 1

Study sites for the soldier crab in Western Australia, ordered north to south

Site number	Geographic location
Site 1	Coconut Well lagoon: margin of dune, ~ 1 m below HAT
Site 2	Coconut Well lagoon: high-tidal creek bank in protected lagoon
Site 3	Entrance Point, Broome: beach slope
Site 4	Town transect, Broome: high-tidal sand flat
Site 5	Nine-mile Creek, Port Hedland: high-tidal creek sandy bank
Site 6	Six-mile Creek East, Port Hedland: base of beach slope
Site 7	Six-mile Creek West, Port Hedland: sandy tidal flat
Site 8	Cossack East, Cape Lambert area: mid-tidal sand flat
Site 9	Settlers Beach, Cape Lambert area: low-tidal sand flat
Site 10	Point Samson, Cape Lambert area: low-tidal sand flat
Site 11	Hearsons Cove # 1, Dampier Archipelago: high-tidal alluvial sand flat
Site 12	Hearsons Cove # 2, Dampier Archipelago: front of mangroves
Site 13	Hearsons Cove # 3, Dampier Archipelago: shore-parallel shoal
Site 14	Withnell Bay, Dampier Archipelago: low-tidal sand flat
Site 15	King Bay # 1, Dampier Archipelago: sand shoal on low-tidal sand flat
Site 16	King Bay # 2, Dampier Archipelago: sand shoal on low-tidal sand flat
Site 17	King Bay # 3, Dampier Archipelago: sand bar on low-tidal sand flat
Site 18	King Bay # 4, Dampier Archipelago: sand shoal in tidal creek
Site 19	Onslow: tidal-creek sandy bank
Site 20	Mangrove Bay, North West Cape: mid-tidal sand flat on pocket beach
Site 21	One Tree Road, Gascoyne Delta: tidal-creek sandy bank
Site 22	West Babbage Island, Gascoyne Delta: tidal creek in lagoon
Site 23	West Babbage Island, Gascoyne Delta: low-tidal sand flat in lagoon
Site 24	Gascoyne Flats, north-eastern Shark Bay: mid-tidal sand flat
Site 25	Monkey Mia, central Shark Bay: low-tidal sand flat

emphasis on populations that are sparse, or determining their environmental limits of occurrence, or on documenting the range of habitats that a species may occupy across its full biogeographic range. We have endeavoured to document as wide a variety of habitats and niches of the Western Australian soldier crab as possible across their biogeographic range, regardless of their population density, and in this context this meant sampling some tidal environments that supported only sparse populations of the species.

Additionally, three sites were studied specifically to show soldier crab distribution in relation to salt marsh and mangroves. These were Sites 1, 5 and 10.

Over time we have observed that, depending on patchy recruitment and/or successful recruitment, the soldier crab populations at a given location may be present or absent on an inter-annual basis. Further, for some locations, the soldier crab habitat is dynamic, and there are changes in elevation or grain size properties inter-annually. Even if present over a number of years at a given locality, *e.g.*, the site at King Bay in the Dampier Archipelago, their population numbers may fluctuate (Unno 2008b). Consequently, because crab densities were used as part of this present study to categorise a soldier crab habitat, we concluded that, where abiotic data were to be collected along with data on crab density, it would not be valid to compare transect data and soldier crab density data collected over a number of different years that may be reflecting variable inter-annual recruitment patterns and habitat dynamics but rather restricted all sampling to the same month and year. Soldier crab recruitment appears to be region-wide, generally occurring predominantly in June–July annually, hence we attempted to partly constrain inter-annual variability and intra-annual variability in populations densities in this study by collecting the data on habitat features along transects and on soldier crab densities all within the same month and year (July 2004). This approach, however, would not circumvent the variability in population densities resulting from variability in recruitment that may have occurred spatially in the region (Unno 2008b).

A second sampling programme to collect data for factor analysis (or Principal Component Analysis) along seven selected transects of the twenty-five study sites was undertaken in July 2007.

Field description of the soldier crab habitat

In the field at each of the twenty-five study sites that were selected for detailed habitat characterisation, the soldier crab habitat was documented in terms of its geomorphic setting at the large scale (> 100 m), medium scale (100 m to 10 m) and small scale (< 10 m). The topography across each soldier crab habitat, from land to seaward, was surveyed during low tide of a spring tide (to ensure that the groundwater under the tidal flat was at its lowest level) in a transect at a scale horizontally of 1–5 m intervals (depending on the complexity of the topography) to a vertical accuracy of 1 cm. The depth of the water table under the tidal flat during the low tide was recorded during the survey. In order to place the soldier crab habitat into context, part of the landscape landward of the tidal flat and seaward of the soldier crab habitat was also included in the topographic and environmental survey where appropriate. This provided information on hinterland characteristics such as the potential of fresh water residing under coastal dunes. Since the majority of the transects were in areas remote from bench marks for datum heights, a system was devised to relate the surveyed transect to AHD. Each transect was related to AHD by surveying the transect to the level of the high or low tide for that day, and referring the water level to the predicted high tide or low tide for that day that the transect was surveyed: that level was used as a temporary datum relative to AHD.

For most of the twenty-five transects, while the transect extended upslope and downslope from the soldier crab habitat, there was a focus on sampling to obtain abiotic and geographical data *within* the confines of the soldier crab habitat. To obtain data for the Principal Component Analysis, seven representative transects (selected from the twenty-five) were fully extended from high tide to low tide, and extensively sampled along the tidal gradient to relate the distribution of soldier crabs to various abiotic parameters (Figure 3), *viz.*, tidal elevation, gradient of shore, sediment types, depth to water table at low tide, and substrate characteristics (in terms of grain size, pellicular water content, salinity of the pellicular water, proportion of silicic grains to calcium carbonate grains, organic matter content in the total sediment, mud content, and organic matter in the mud). These transects were at Point Samson, Settlers Beach, East Cossack, Hearsons Cove landward of the mangroves, Hearsons Cove shore-parallel shoal, King Bay shoal # 3, and Mangrove Bay.

Microtopography (involving features < 30 cm high, such as hummocks and small sand ripples), was also noted as it was observed that they influence the location of workings of the soldier crabs for a given day. For Sites 12 and 13, detailed topographic levelling was undertaken to determine the nature of the mounds and depressions at these sites, to document the level of the groundwater table (at low tide) under the undulating tidal-flat surface, and to relate crab workings to the microtopography.

At each of the sampling sites along the transects, five replicate samples of approximately 100 g of sediment were collected from the sediment surface (0–2 cm deep) for granulometric analysis, determination of quartz and calcium carbonate content, and determination of content of organic carbon, pellicular water, and salinity of pellicular water. The sediment was hermetically sealed in the field, and frozen for transport and storage. Groundwater was collected from shallow pits excavated in the tidal flat within the soldier crab zone. The salinity of open waters that recharge tidal-flat groundwater and pellicular water can determine the salinity of the latter, and so open oceanic waters or open tidal-creek waters that flooded the tidal flat on a high tide were sampled as a baseline of the source waters. Three such samples were collected.

Population abundance in the soldier crab habitat in the centre of each transect site was determined by excavating five randomly-placed box cores (25 cm x 25 cm x 15 cm deep), and sieving out the crabs through a 1 mm mesh (see Unno 2008b). The population abundance was categorised for the regional sites as high (> 400 crabs per m^2), medium (399–100 crabs per m^2) or low (< 100 crabs per m^2). The occurrence of soldier crabs with respect to tidal level was determined by surveying and

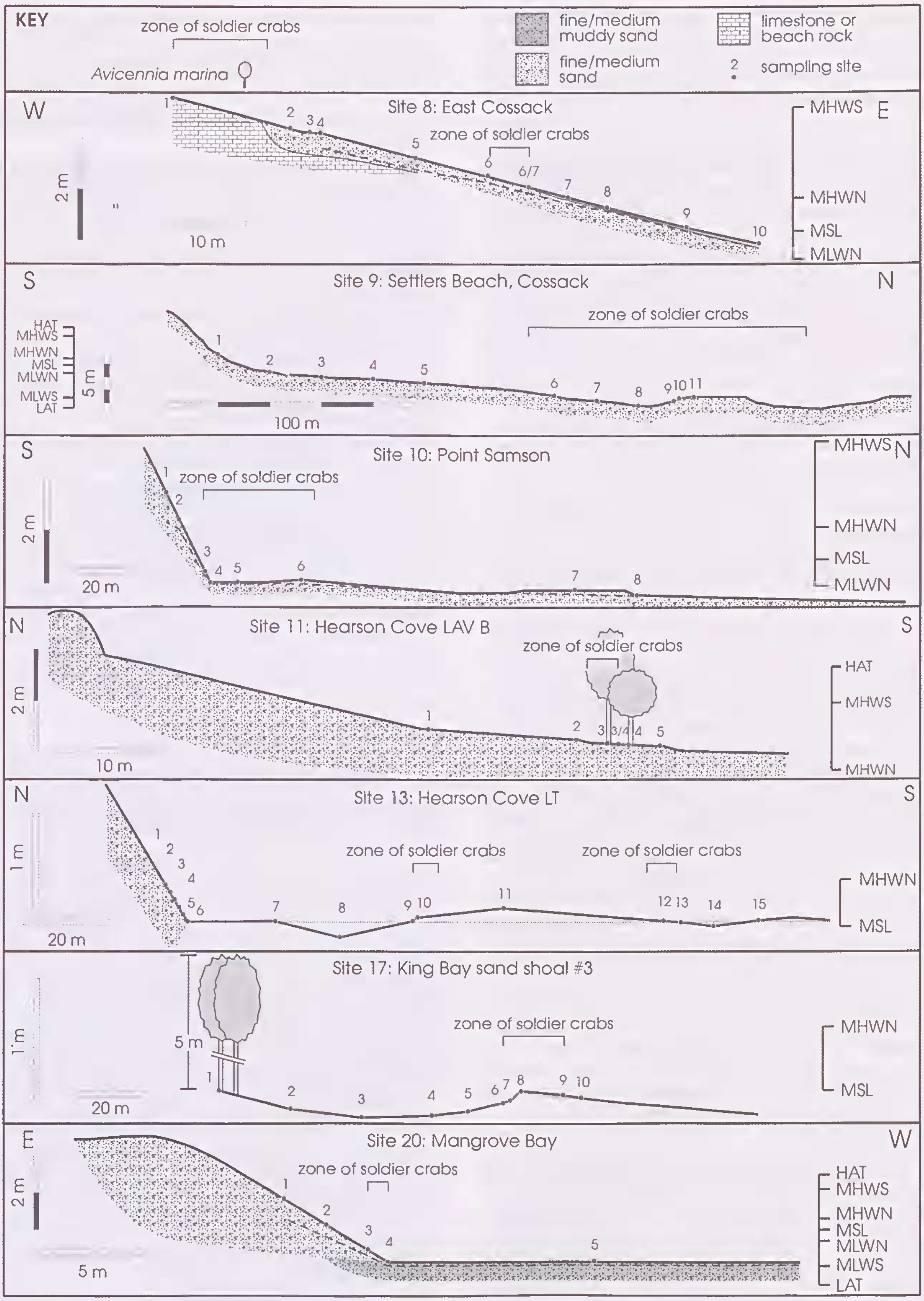


Figure 3. Seven transects used to obtain data in the Principal Component Analysis, showing transect profile with respect to tidal levels and sampling points. The data on groundwater salinity, pellicular water salinity, organic matter content of sediment, content of mud, organic matter content of mud, sediment moisture at low tide, and depth to groundwater at low tide obtained from the sampling points are tabulated in Appendix 2.

noting their presence/absence and relative abundance of surface workings along the transect. Relative abundance of surface workings was categorised by percentage cover of sediment surface as follows: dense (100–50%), medium (49–10%) and sparse (< 10%).

This study focused on describing the variety of habitats of the soldier crab and the prevailing abiotic characteristics that occurred within habitats. The intent was to determine the environmental features that were characteristic of the soldier crab habitat rather than a study across the entire tidal flat to determine the boundary of the soldier crab habitat in detail. Hence, apart from the seven transects mentioned earlier, the sampling of sediment for grain size, pellicular water content, and pellicular water salinity was not undertaken incrementally along the entire transect across the tidal flat but only *within* the main body of the soldier crab habitat. However, the environmental variability within the soldier crab habitat for the parameters of grain size, pellicular water content, and pellicular water salinity was determined because the replicate sampling was extensive across the area where soldier crabs occurred for a given site.

Experimental work to define soldier crab sediment preferences

To determine the sediments that soldier crabs preferred and avoided, experimental sediment blocks were emplaced within their habitat at Site 15, where soldier crabs have been observed over 30 years to be consistently present and abundant. Four blocks of exotic sediment of four different sediment types, *viz.*, mud, muddy sand (with ~ 30% mud), shell grit, and shell fine gravel, and five control blocks of local sand (sieved free of crabs) obtained from the soldier crab habitat, were artificially emplaced into excavated square pits 25 cm x 25 cm x 25 cm deep on the sandy tidal flat where soldier crabs were abundant, so that the top of the block of emplaced sediment was contiguous with the surface of the tidal flat. The south-eastern corner of each block of sediment was marked by a 1 cm diameter wooden dowel, pushed into the sediment so that each block could be located later. The activity of the crabs across that portion of the soldier crab habitat, where the experiment was conducted, was documented daily for a week, and then revisited on a 3-monthly basis for one year. Crab activity for the first week, and on the three-month basis, was assessed by the presence, if any, of biogenic structures (such as single pustules, pustular structures, exit holes, or re-entry rosettes; Unno & Semeniuk 2008). A year later, the exotic blocks of sediment and the natural (control) blocks of sediment were excavated and sieved in the field to determine the presence or absence of soldier crabs therein.

In addition, along some transects, where soldier crab density dropped to zero across a change in sediment type but not in other abiotic characteristics *(e.g.,* from sand, with occurrence of soldier crabs, to gravel, grit, muddy sand, or mud, all with an absence of soldier crabs), samples of the latter sediments were collected for analyses to characterise the granulometry of sediment that the crabs appeared to avoid.

Finally, in addition to the sampling described above, and that undertaken along the transects, in a general regional sampling programme, wherever soldier crabs occurred, a sample of the habitat sediment was collected to ascertain modal grain size and mud content to determine the range of sediment types that soldier crabs inhabited.

Methods to determine if plant roots influence soldier crab occurrence

At two locations where soldier crabs inhabited sandy substrates within or proximal to mangroves (*Avicennia marina*), the possible influence of mangrove cable roots and root hairs on soldier occurrence was investigated. These were Site 5 (at Nine-mile Creek), and Site 10 (at Hearsons Cove landward mangrove zone). Five replicate box core samples, 25 cm x 25 cm x 20 cm in size, were excavated within the zone that soldier crabs occupied (where generally there were sparse roots of mangroves), five replicate samples were also obtained where the mangrove roots were abundant and there was an absence of soldier crabs, and five replicate samples were obtained mid-way between these two sampling sites. To obtain the root samples, pneumatophores above the sediment surface were trimmed to ground level, and the sediment in the box core then excavated to ensure that only the biomass of pneumatophores and root matter below the ground would be estimated. The material excavated from the box cores was washed through a 3 mm sieve to isolate the mangrove pneumatophores, cable roots, and root hairs. Later, the root matter was oven-dried and weighed. The same sampling procedure was carried out for another plant, *i.e.*, the sea couch, *Sporobolus virginicus*, at Site 1 (at the Coconut Well dune margin), again, focusing on collecting only the root matter below the sediment surface

Laboratory analyses

In the laboratory, the granulometry of the sediment was determined by wet sieving the sediment at 1 phi intervals (Wentworth 1922). Organic carbon and calcium carbonate content of the total sediment were determined by combustion, *i.e.*, loss on ignition (Gross 1971). The determination of organic matter for the *whole of sediment* involved organic matter in the > 63 mm fraction as well as that in the < 63 mm fraction and did not allow for differentiation between interstitial flora (McLachlan 1990b), interstitial fauna (McLachlan 1990c), and plant detritus. After sieving, the mud fraction was processed further: its organic carbon content was determined by combustion. The determination of organic matter within the mud fraction did not differentiate between interstitial flora such as diatoms, fungi, bacteria and detritus (McLachlan 1990b), all possible food particles that could be entrained by soldier crabs while feeding. Pellicular water content of the sand was determined by gravimetric method by weighing wet sediment, drying it, and reweighing the dried sediment. Salinity of pellicular water was determined using the method of C A Semeniuk (2007): after weighing, the wet sand was dispersed in 100 ml of de-ionised water and the salt content of the 100 ml of water then determined by an electrical salinometer (a CyberScan 200 TDS meter); the sand was then rinsed with de-ionised water, the water decanted, the sediment dried and weighed; the salinity of pellicular water was determined by calculation of total salt content with respect to the moisture content of the sand. Groundwater salinity and marine water salinity were determined in parts per thousand (ppt) using an electrical salinometer.

Pneumatophores and root matter from *Avicennia marina* and *Sporobolus virginicus*, retrieved from sieving, were dried and weighed to determine root matter content per m^2.

Field Assessment of exposure/shelter for sandy coasts

There is varied use of the terms "exposed" and "sheltered" and "high energy" and "low energy", and to provide a relatively consistent measure of these terms, Brown (1990) proposed a general classification scheme of degree of exposure of sandy shorelines or sandy beaches by aggregating scores obtained from a range of criteria that included wave action, surf zone width, intertidal slope in combination with median grain size, % of very fine sand, median particle diameter, depth of reduced layer, and animals with permanent burrows. Based on a score between 1–20 (with 1 being low energy and 20 being high energy), the classification scheme resulted in the categorisation of beaches into four types: very sheltered (with virtually no wave action, reduced sediment layers in the shallow subsurface, and abundant macrofaunal burrows); sheltered with little wave action, reduced sediment layers present in the subsurface, and usually some macrofaunal burrows); exposed (with moderate to heavy wave action, reduced sediment layers deep in the profile and usually no macrofauna in burrows); and very exposed with heavy wave action, no reduced sediment layers and macrofauna consisting of highly-mobile forms only).

While in detail there are difficulties and complications with applying the system devised by Brown (1990), as will be discussed below, to provide a relative measure in an international comparison of the degree of exposure of the twenty-five study sites, we applied criteria devised by Brown (1990) to coasts in the study area.

Brown's (1990) classification has not allowed for sandy coasts that are partly reflective in upper tidal zones, and partly dissipative in lower tidal zones (Wright & Short 1983; and see later). This means that the intertidal slope in many locations cannot be graded as a single value where there are two or three slope values along the tidal gradient. For purposes of this study, we selected the slope gradient for that part of the beach or sandy shore wherein resided the soldier crabs. Additionally, in being devised (implicitly) for use only for sandy shores with offshore bars and shoals where waves may first break, the scheme, in its application of waves impinging upon shore, does not allow for the ranking of any geologically/ geomorphically-complex coasts and bathymetrically-complex coasts (*e.g.*, where low-lying limestone barriers provide the partial shelter, or where a tidal creek along a sandy barrier coast comprises the sheltered environment). There also is a problem in applying some of the criteria that are used to denote strong wave action (*viz.*, depth of the reduced sedimentary layer, or grain size distribution) when it may be strong tidal currents that are mobilising the sediment rather than waves, or where there is a change in sediment grain size, or change in depth to the zone of anoxia across the tidal gradient.

Nonetheless, the scheme of Brown (1990) does provide a broad measure of high-energy coast *versus* low-energy coast, and since most of the coasts in this study are more or less sandy, we have applied the scheme to the twenty-five study sites to determine where they fit in the energy spectrum.

Tidal level and tide style information

Since soldier crabs at a specific locality can inhabit tidally exposed surfaces from ~ HAT to ~ MLWN, in microtidal to mesotidal to macrotidal and extreme macrotidal settings, noting the position of the habitat with respect to AHD or MSL is not meaningful. We adopted an approach by which frequency of flooding was determined, *i.e.*, the percentage of time that a particular level is submerged, regardless of tidal range. This method provides a better assessment of the factors that underpin soldier crab occurrence in that it gives a measure of the conditions of submergence or inundation to which soldier crabs are subjected. Graphs showing frequency of flooding (or submergence curves) for major ports in the study area, *viz.*, Broome, Port Hedland, Cape Lambert (Port Walcott), Dampier, Onslow, Learmonth, and Carnarvon were supplied by the Department of Planning and Infrastructure (Government of Western Australia), and these were used to determine the frequency of flooding of a soldier crab habitat along a given transect.

Data analyses

Statistical methods employed in the paper included determining the mean and standard deviation of population abundance, and mean values of other parameters that were sampled in replicate. Further analyses involved bivariate linear regressions, multiple linear regressions and transformed linear regressions for use in Principal Component Analysis. Bivariate linear regressions were carried out on abundance of crabs (*i.e.*, crabs/m^2) regressed each in turn on groundwater salinity, pellicular water salinity, sediment moisture, sediment organic carbon content, mud content, and organic matter in mud. Mud content was also regressed on organic matter in mud using data from the soldier crab habitats sampled at the twenty-five transects. The parameters selected for regression (*viz.*, groundwater salinity, pellicular water salinity, sediment moisture, and mud content) are not strictly independent variables. That is, tidal level determines groundwater salinity *and* pellicular water salinity with increase in salinity of both upslope along the tidal gradient (thus, groundwater salinity and pellicular water salinity are related); groundwater salinity can influence pellicular water salinity, mud content and moisture content are both related to the tidal gradient, and mud content can affect moisture content. The relationship between crab numbers and an individual abiotic characteristic was not linear, consequently, direct linear regression to relate crab abundance to individual abiotic was too simplistic. This is consistent with crabs having an optimum or preferred range of salinity, moisture, mud content, and so on.

Because the initial scatter plots showed a weak to moderate association with abundance which seems due to some environmental data values skewing in relation to the optimal range of the crab, a second technique (transformed linear regressions) was used wherein the deviation from a projected mean or trend was assessed, and values to the positive side of the projected trend were rotated (transformed) into a single trend, and regressed again. For each environmental parameter, its optimal value (or range) for supporting high crab abundance was estimated. The difference between the estimates from each observed value of the parameter was calculated. The abiotic environmental parameters contribute jointly to the overall probability (*i.e.*, proportion) of the maximum possible crab abundance that would exist under optimal conditions. The overall probability is the product, not the sum, of the individual probabilities contributed by the parameters. At, say, a given transect, if one or more of the parameters contribute a zero probability, then the overall probability is zero for the transect no matter how optimal the other parameter values are at that transect. For example, if salinity is fatally high, then there will be no living crabs no matter how optimal the other parameters. Therefore, the relationship between abundance and the parameters was modelled to reflect how the individual probabilities vary with the environmental parameters. That is, as environmental parameters deviate from optimal, the model should predict the % drop in abundance. Such a model would need to correspond to the necessarily multiplicative derivation of the overall probability or proportion of abundance.

For Principal Component Analysis, data from the sampling sites from the seven transects (Figure 3) were used, *viz.*, abundance of crabs, groundwater salinity, pellicular water salinity, sediment moisture sediment modal grain size, sediment organic carbon content, sediment mud content, organic matter in mud, depth to water table at low tide, % grain size 500 mm, % grain size 250 mm, % grain size 125 mm, and % grain size 63 mm (Appendix 2). Orthogonal (Varimax) and oblique (Direct Oblimin) rotations were utilised, as well as PRIMER 6® (Plymouth Routines in Multivariate Ecological Research).

Regional setting of study sites

The twenty-five transect sites extend across a latitudinal distance of approximately 900 km, and 8º of latitude, spanning several climatic, coastal, and oceanographic zones. In order to document the variety of soldier crab habitats in the biogeographic range of the species, and place each habitat into a regional context, the large-scale characteristics of climate (such as temperature, rainfall, evaporation, and humidity), coastal sectors and oceanography (sea temperatures and tidal ranges) for each site are described in Table 2 and summarised below. This information on coastal sector setting, climate setting, rainfall, evaporation, air temperature and sea surface temperature, and tides is provided as background for the soldier crab habitats of the various transect sites, and for use for comparative purposes by other researchers on *Mictyris* elsewhere, and, in addition, to provide background information on the variation in the regional environment of *M. occidentalis*.

The study sites span three climate zones (Gentilli 1972; Australian Bureau of Meteorology 1995): tropical semi-arid for the Broome sites, tropical arid for Port Hedland, Cape Lambert, Dampier Archipelago, Onslow sites, and North West Cape sites, and subtropical arid for the Gascoyne Delta and Shark Bay sites. All sites experience hot summers and, for most of the area, particularly progressing from southern sites to northern sites, rain is delivered by cyclones and thunder storms in summer. Mean air temperatures range from a maximum of 33.2 °C at Port Hedland, to a minimum of 16.6 °C at Carnarvon. Mean annual rainfall ranges from 575 mm at Broome, to 225 mm at Carnarvon and Shark Bay. Mean annual evaporation ranges from 3400 mm at Dampier Archipelago and Cape Lambert, to 2800 mm at Carnarvon and Shark Bay. Mean annual humidity (3 pm) is highest at 62% in Carnarvon and Shark Bay and lowest at 34% in the Cape Lambert area. Mean sea surface temperatures at the regional study sites vary from a high of 29.4 °C at the Broome sites in the north to a low of 21.5 °C at the Carnarvon and Shark Bay sites to the south.

Soldier crabs inhabit three coastal sectors: the Canning Coast, the Pilbara Coast and the Carnarvon Province (Semeniuk 1993), all with their differing geomorphic units expressed at the smaller scale (Semeniuk 1986): along the Canning Coast and Pilbara Coast there are tidal embayments, tidal lagoons, tidal creeks, shoals, base of beach slopes, low tidal sand flats, and ebb-tidal deltas; in the Carnarvon Province there are tidal lagoons, tidal creeks, depressions leeward of spits, and the base of beach slopes. Tides in the study area between North West Cape and Broome are semi-diurnal. Tides at Houtman Abrolhos, Carnarvon, and Shark Bay are variable: Carnarvon is mixed semi-diurnal and diurnal; Monkey Mia is predominantly semi-diurnal; Houtman Abrolhos is predominantly diurnal. Tidal ranges are extreme macrotidal (mean tidal range > 8 m; *cf.* Semeniuk 2000) for sites between Port Hedland and Broome, macrotidal (mean tidal range > 4 m up to 8 m) for Dampier Archipelago and the Cape Lambert area, mesotidal (mean tidal range 2–4 m) at Onslow and North West Cape, and microtidal (mean tidal range ≤ 2 m) at Houtman Abrolhos, Shark Bay and Carnarvon.

Wave energy in relation to shore types and soldier crab habitats

In terms of the regional- to local-scale setting and wave energy, it is evident that soldier crabs occupy habitats that are relatively low energy, *i.e.*, either sheltered from direct wave action, or subject to diminished wave action due to offshore dampening effects (*e.g.*, seagrass meadows, or low-gradient, dissipative shores). In this context, most of the study sites with resident soldier crabs are generally in relatively low wave-energy environments because of their location in embayments, barred tidal lagoons, tidal creeks and tidal lagoons within strand plains and deltaic complexes, and beach/dune shores leeward of spits or rocky headlands. Local-scale habitats (geomorphic units) within these relatively low wave-energy environments are comparatively stable and less prone to major sediment movement and surface sediment reworking by strong wave action, and hence host a range of infaunal organisms (including soldier crabs) that reside within the upper 30 cm of the substrate.

However, within these environments, some sites are more, or less, sheltered than others: Table 3 provides a

Table 2

Description of location and regional features of study sites including coastal sector, climate setting, rainfall, evaporation, air temperature and sea surface temperature and tidal information (Data sources: Australian Bureau of Meteorology 1995; Australian National Tide Tables 2009)

Sites 1–4: Sites 1 and 2 Coconut Well (17° 49' 16.0", 122° 12' 45.38") ~ 18 km north of Broome, Site 3 at Entrance Point, Broome (17° 59' 53.72", 122° 12' 25.99"), and Site 4 at Broome boat ramp (17° 58' 02.41", 122° 14' 12.71") facing southern Roebuck Bay are all in the same climatic and oceanographic zone along the Canning Coast. Climate is tropical, semi-arid, with hot summers, and with summer rainfall; mean annual rainfall 575 mm; mean annual evaporation 3200 mm; mean annual humidity (3 pm) is 50%; mean annual temperature range 32.1°C – 21.1°C; and mean sea surface temperature range 29.0°C – 23.4°C. Tides semi-diurnal and macrotidal; tidal ranges are: HAT-LAT = 10.5 m; MHWS-MLWS = 8.3 m; MHWN-MLWN = 2.1 m
Sites 5, 6 and 7 at Port Hedland are located at Nine-mile Creek (20° 20' 1.03", 118° 40' 18.83"), Six-mile Creek West (20° 19' 19.42", 118° 39' 50.72"), and Six-mile Creek East (20° 19' 19.42", 118° 39' 50.72"), respectively, are on the Pilbara Coast. Climate is tropical, arid with hot summers, and with summer rainfall; mean annual rainfall 311 mm; mean annual evaporation 3300 mm; mean annual humidity (3 pm) is 39%; mean annual temperature range 33.2°C – 19.4°C; tidal ranges are: HAT-LAT = 7.5 m; MHWS-MLWS = 5.5 m; MHWN-MLWN = 1.3 m
Site 8, 9 and 10 are at Cossack East (20° 40' 30.92", 117° 11' 38.08") along Butchers Inlet, east of Cossack, Settlers Beach (20° 40' 03.20", 117° 14' 40.24") north of Cossack, and at Point Samson (20° 37' 47.46", 117° 11' 51.04"), respectively; are on the Pilbara Coast. Climate is tropical, arid; with hot summers and summer rainfall; mean annual rainfall 313 mm; mean annual evaporation 3400 mm; mean annual humidity (3 pm) is 34%; mean annual temperature range 31.9°C – 20.1°C; and mean sea surface temperature range 28.4°C – 24.1°C. Tides are semi-diurnal and macrotidal; tidal levels from nearest port (Port Walcott) are: HAT-LAT = 6.2 m; MHWS-MLWS = 4.3 m; MHWN-MLWN = 1.1 m
Sites 11–18 are in the same climate and oceanographic region in the Dampier Archipelago along the Pilbara Coast. Sites 11, 12, and 13 are at Hearsons Cove (20° 37' 37.63", 116° 47' 53.11"), Site 14 is at Withnell Bay (20° 34' 17.87", 116° 47' 46.68"), Sites 15–18 are in King Bay (20° 38' 0.8.56", 116° 45' 26.21"; 20° 38' 10.84", 116° 45' 29.35"; 20° 38' 8.63', 116° 45' 35.06"; 20° 38' 13.52", 116° 45' 28.85"). Climate is tropical arid; with hot summers, and with summer rainfall; mean annual rainfall is 311 mm; mean annual evaporation is 3400 mm; mean annual humidity (3 pm) is 51%; mean annual temperature range is 30.6°C – 22.7°C; and mean sea surface temperature range is 28.4°C – 24.1°C. Tides are semi-diurnal and macrotidal; tidal ranges are: HAT-LAT = 5.1 m; MHWS-MLWS = 3.7 m; MHWN-MLWN = 0.9 m
Site 19 is at Onslow (21° 41' 02.85", 115° 03' 23.50") along the Pilbara Coast. Climate is tropical, arid; with hot summers, and with summer rainfall; mean annual rainfall 275 mm; mean annual evaporation 3000 mm; mean annual humidity (3 pm) is 54%; mean annual temperature range 31.3°C – 18.1°C; and mean sea surface temperature range is 27.6°C – 24.5°C. Tides are semi-diurnal and mesotidal; tidal ranges are: HAT-LAT = 3.0 m; MHWS-MLWS = 1.9 m; MHWN-MLWN = 0.6 m
Site 20 is at Mangrove Bay (21° 58' 17.17", 113° 56' 24.89") is on the western side of North West Cape, Carnarvon (coastal) Province. Climate is tropical, arid; with hot summers, and with autumn-winter rainfall; mean annual rainfall 267 mm; mean annual evaporation 3000 mm; mean annual humidity (3 pm) is 35%; mean annual temperature range 30.8°C – 19.1°C; and mean sea surface temperature range is 30°C – 17°C. Tides are semi-diurnal and mesotidal; tidal ranges are: HAT-LAT = 2.8 m; MHWS-MLWS = 1.8 m; MHWN-MLWN = 0.6 m
Sites 21, 22, 23 and 24 are in the same climate and oceanographic region in the Carnarvon (coastal) Province: Site 21 is at One Tree Point (24° 51' 43.88", 113° 37' 43.00" on a strand plain north of Carnarvon, Site 22 is at West Babbage Island, Gascoyne Delta (24° 52' 36.60", 113° 37' 34.46"), and Site 23 is at West Babbage Island, Gascoyne Delta (24° 52' 38.74", 113° 37' 30.72") west of Site 22, and Site 24 is the tidal edge of the Gascoyne Flats, (24° 54' 44.71", 113° 40' 17.88"), northeast of Shark Bay. Climate is subtropical and arid; with hot summer and autumn-winter rainfall; mean annual rainfall 230.8 mm; mean annual evaporation 2800 mm; mean annual humidity (3 pm) is 62%; mean annual temperature range is 27.2°C – 16.6°C; and mean sea surface temperature range is 25.3°C – 21.5°C. Tides are mixed semi-diurnal and diurnal, and microtidal; HAT-LAT = 2.0 m; MHWS-MLWS = 0.9 m; MHWN-MLWN = 0.5 m
Site 25 is at Monkey Mia (25° 47' 36.44", 113° 43' 18.05") on the east side of the Peron Peninsula, Shark Bay, Carnarvon (coastal) Province. Climate is subtropical, arid; with hot summers and autumn to winter rainfall; mean annual rainfall is 224.7 mm; mean annual evaporation 2800 mm; mean annual humidity (3 pm) is 62%; mean annual temperature range is 26.6°C – 17.5°C; and mean sea surface temperature range is 25.0°C – 21.5°C. Tides are predominately semi-diurnal and microtidal; tidal ranges are: HAT-LAT = 1.5 m; MHWS-MLWS = 1.0 m; MHWN-MLWN = 0.4

ranking of exposure to wave energy at the study sites, graded from regionally most exposed to most sheltered, based on geomorphic considerations (such as barriers), slope characteristics of the tidal zone, occurrence of mud in the sediments, grading of grain size upslope, and observation of wave types. Table 3 also provides an explanation for the occurrence of the soldier crab habitat at each of the twenty-five study sites.

For this study, three types of exposure/shelter, based on degree of wave exposure, energy of the waves, and degree of geomorphically-controlled shelter, are identified (Table 3). Type 1, which is regionally exposed, is where the whole coast is open and exposed to swell and wind waves; this coastal type may be locally dissipative with respect to wave energy and hence generating low-gradient flats; Type 2, although the regional context is of exposure to waves, is where the local environment is reasonably sheltered, hence of lower energy than the open coast; and Type 3 is fully sheltered, however, while the open coast may be regionally exposed to swell and wind waves, the site or habitat is wholly protected from these waves. Soldier crabs occurring in Type 1 coastal setting do so because of the shoal and depression tidal topography, local shelter along exposed coasts by offshore ridges, or shelter amongst rocky knolls or outcrops (*e.g.*, semi-protected sand pockets leeward of, or amongst, local rock outcrops on a high-energy beach such as Entrance Point at Broome). Soldier crabs occurring in Type 2 sites do so because of local shelter along exposed coasts, leeward of permanent mangrove-vegetated sand shoals such as at King Bay (Dampier Archipelago), leeward of low shoals and spits in shoal-and-spit complexes along low-gradient, dissipative shores such as at Settlers Beach (Cape Lambert region) and Monkey Mia (Shark Bay), or leeward of seagrass banks that have absorbed much of the wave energy of translational waves such as at the shore of the Gascoyne Flats (north-eastern Shark Bay). Soldier crabs occurring in Type 3 sites occur in lagoons or on strand plains fully protected from open coastal swell and wind waves by barriers (*e.g.*, the sites at Coconut Well, and on the strand plain of the Gascoyne Delta).

Application of the criteria of Brown (1990) to assess exposure/shelter, as described earlier in the Methods, results in the categorisation of the twenty-five study sites as sheltered to very sheltered (Table 4). The grading of the coasts in terms of wave energy presented in Table 3 is more or less supported by the application of the criteria of Brown (1990), with Entrance Point (Broome) being assessed as most exposed, and the (coastally invaginated) tidal creeks and lagoons (axiomatically) being assessed as most sheltered.

Various degrees of wave energy generate different types of beaches, sandy shores, and beach forms. Wright & Short (1983) have categorised the types, identifying at one extreme, reflective beaches and at the other extreme, dissipative beaches, together with a range of intermediate forms.

In north-western Australia, in the biogeographic range of *M. occidentalis*, macrotidal sandy shores commonly show a partitioning of slope, with a steeper shore between ~ MSL and HAT (gradients ~ 1:30 to 1:50), and a low-gradient shore between ~ MSL and LAT (gradients ~ 1:100 to 1:200). The upper, steeper part of the shore is referred to as a reflective beach (Wright & Short 1983). Commonly, the reflective beach sharply adjoins the low-gradient part known as the dissipative beach (Wright & Short 1983; Short & Wright 1984), and as such, most macrotidal sandy shores in north-western Australia can be assigned to the intermediate beach type, comprised of a high-tidal reflective domain and a low-tidal dissipative domain (Figure 4).

Table 3

Exposure to wave-energy ranking and explanation for occurrence of soldier crab habitat at each of the twenty-five study sites

Soldier crab habitat site	Exposure	Explanation for relative shelter and development of soldier crab habitat
High wave energy – most exposed coasts – Type 1 coast		
Entrance Point, Broome	regionally exposed; very locally sheltered	a peninsula of Mesozoic rock fully shelters the site from waves deriving from south-westerly to north-easterly quadrants, and partially shelters the sites from waves deriving from southerly quadrants; on the beach, at the local scale, Mesozoic rock outcrops provide pockets of relative shelter for soldier crab habitat
Settlers Beach near Cape Lambert	regionally semi-protected; locally protected by shoals and spits	a rocky peninsula of Precambrian rock on the east of the site semi-protects this site regionally from easterly swell, and Cape Lambert protects the site from westerly and north-westerly swell; low-tidal zone is a dissipative shore and hence, locally, the soldier crab habitat is protected by emergent shoals and spits
Point Samson near Cape Lambert	regionally semi-protected; locally protected by shoals and spits	a rocky peninsula of Precambrian rock on the east of the site and Pleistocene limestone on the west shelter this embayment from ocean swell and most wind waves
Six-mile Creek West, and Six-mile Creek East, Port Hedland	regionally exposed; sub-regionally sheltered	a line of Quaternary limestone reefs partially shelters these sites from ocean swell; low-tidal zone is a dissipative shore
Moderate wave energy – coasts exposed to local wind waves, but with local protection – Type 2 coast		
Mangrove Bay, north-western North West Cape	regionally protected from swell by the Ningaloo Reef and from wind waves by a barrier spit – effectively the site is along the shore of a semi-barred lagoon	the Ningaloo Reef and the alongshore barrier spit combine to protect the semi-barred lagoon
Gascoyne Flats, north-eastern Shark Bay	regionally protected by offshore limestone islands; sub-regionally exposed to local wind waves	offshore seagrass banks dampen wave energy at this site

Monkey Mia, middle Shark Bay	regionally protected by offshore limestone islands and Peron Peninsula; sub-regionally exposed to local wind waves; locally protected by spit	while sub-regionally wave-agitated, locally emergent shore-parallel large sand spit protects this site
Broome Town	regionally sheltered in large embayment	a peninsula of Mesozoic rock (comprising the Broome Peninsula – Gantheaume Point and Entrance Point) fully shelters the site from waves deriving from south-westerly to north-easterly quadrants, and partially shelters the site from southerly waves; at the local scale, mangroves seaward of the high-tidal sand flat also shelter these sites
Hearsons Cove sites # 2 and 3, Dampier Archipelago	regionally semi-exposed in wide embayment	large rocky headland of Precambrian rock provides protection from swell and most wind waves; low-tidal zone is a dissipative shore and hence, locally, the soldier crab habitat is protected by emergent shoals
Withnell Bay and King Bay sites # 1–3, Dampier Archipelago	regionally exposed, but sub-regionally protected by long embayment and headlands at narrow mouth of embayments	located deep within the King Bay and the Withnell Bay embayments; further, the King Bay sites are locally sheltered by mangrove-vegetated sand shoals
Hearsons Cove # 1, Dampier Archipelago	high tidal sand flat regionally semi-exposed in wide embayment; locally sheltered by mangroves	a large rocky headland of Precambrian rock provides protection from swell and most wind waves
Low wave energy – coasts protected from waves by barriers, beach ridges (on a strand plain), or sites within tidal creeks – Type 3 coast		
East Cossack near Cape Lambert	regionally semi-protected; tidal flat sub-regionally sheltered by its location at the mouth of a large tidal creek	a peninsula of Precambrian rock and interior of tidal creek combine to provide shelter for this embayment from swell and most wind waves
King Bay # 4 (tidal-creek shoal), Dampier Archipelago	tidal creek shoal regionally exposed, but sub-regionally protected by long embayment and headlands at narrow mouth of embayments	located deep within the King Bay embayment and further sheltered by being in the axis of a tidal creek
Nine-mile Creek, Port Hedland	regionally exposed; sub-regionally sheltered	a line of Quaternary limestone reefs partially shelters these sites from ocean swell and waves; otherwise, shelter afforded by the site being in the axis of a tidal creek
Onslow	tidal creek regionally sheltered by barrier dune	tidal creek is protected from open oceanic wave action and wind waves and shelter also afforded by the site being in the axis of a tidal creek, but may be intermittently subjected to tidal flows
Babbage Island: tidal lagoon and tidal creek within the Gascoyne River Delta	regionally exposed, and sub-regionally well protected by barriers of low dunes and beach ridges; locally protected by shoals and spits	while regionally wave-agitated, extensive deltaic strand plains of low beachridges and local low dunes shelter these sites as lagoons
One Tree Point, Gascoyne Delta	regionally sheltered	within the deltaic complex, this tidal creek is protected from open oceanic wave action and wind waves by barrier dunes; shelter also afforded by the site being in the axis of a tidal creek on a strand plain
Coconut Well (2 sites), Broome	regionally very well sheltered	located in a wholly protected, shallow-water lagoon, sheltered from all oceanic waves by a sand barrier

Wright *et al.* (1982) specifically investigated the partitioning of shore slope along a macrotidal sandy coast at Cable Beach (Broome). They noted the low gradient, dissipative subtidal and low-tidal zone, and the steeper, more reflective mid-tidal and high-tidal zone. With direct measurements of energy flux, and relating wave energy to tidal landforms, Wright *et al.* (1982) concluded that the work of waves over the lunar half cycle for different points on the intertidal profile shows similar dissipation rates and a relatively uniform distribution of work of waves over most of the profile. The maximum of wave work is in the middle of the low-

Table 4

Application of criteria of Brown (1990) in assessing degree of exposure/shelter of a sandy shore for the twenty-five transect sites of this study

Site (graded in order of decreasing energy according to Table 3)	Numerical score of exposure/ shelter using Brown (1990)	Assessment of exposure/ shelter using Brown (1990)
Entrance Point, Broome	10	sheltered
Settlers Beach near Cape Lambert	6	sheltered
Point Samson near Cape Lambert	6	sheltered
Six-mile Creek West, and Six-mile Creek East, Port Hedland	6	sheltered
Mangrove Bay, north-western North West Cape	7	sheltered
Gascoyne Flats, north-eastern Shark Bay	9	sheltered
Monkey Mia, middle Shark Bay	9	sheltered
Broome Town	6	sheltered
Hearsons Cove sites # 2 and 3, Dampier Archipelago	6	sheltered
Withnell Bay and King Bay sites # 1-3, Dampier Archipelago	4 (to 5)	very sheltered
Hearsons Cove # 1, Dampier Archipelago	3	very sheltered
East Cossack	4	very sheltered
King Bay # 4 (tidal-creek shoal), Dampier Archipelago	5	very sheltered
Nine-mile Creek, Port Hedland	5	very sheltered
Onslow	3	very sheltered
Babbage Island: tidal lagoon and tidal creek within the Gascoyne River Delta	3	very sheltered
One Tree Point, Gascoyne River Delta	3	very sheltered
Coconut Well (2 sites), Broome	3	very sheltered

tidal zone and over the lower part of the high-tidal zone. Most of the work of the waves over the low-tidal and mid-tidal zones was performed by unbroken shoaling waves rather than surf zone processes. This is an important factor, as it results in low-gradient shores or low tidal flats (wave-dissipating, and hence wave-smoothed), and steeper shores (that may become reflective beaches) signalling more typical surf-zone processes.

The beach study site of Wright *et al.* (1982) at Cable Beach is high energy, and does not support soldier crabs. Using the scheme of Brown (1990), the beach scores 11, and is assessed as exposed (see later).

In general, in north-western Australia, for sites protected from direct swell, our observations are that during a rising tide, with wind waves (which tend to be low amplitude < 1 m height), the low-gradient slope dissipates wave energy, and when water level is above MHWN, the low-gradient slope of the dissipative shore may be below wave base. The low tidal flats, having dissipated wave energy in low tide and subtidal environments, and *below wave base during high tide*, are subject only to relatively low wave energy and are able to develop soldier crab habitats, particularly if the tidal flat between MSL and MLWN is comprised of shore-parallel shoals. During high tide, with wind waves, the steeper, upper part of the sandy tidal zone (the reflective beach) receives and partly reflects wave energy, and is a higher energy zone of the shore. Such steeper shores generally do not support soldier crab populations for reasons of wave energy, and depth to water table during a low tide. Also, they tend to be coarser in grain size than the low tidal flats. However, since the upper part of the beach slope acts as an aquifer for high tide phreatic seawater, which discharges during ebb tide from the beach face along the contact between the relatively steep slope and the low-gradient slope, there is local development of soldier crab habitat either along the base of the slope of these reflective beaches (if their grain size is not too coarse) or on the sand flat immediately adjoining the beach slope.

Figure 4. Hearsons Cove showing low-gradient dissipative shore (a low-tidal flat) sharply adjoining a steeper-gradient, higher-tidal reflective beach.

Coastal sediments, hydrology, salinity, vegetation, and stratigraphy

A brief and simplified synthesis is provided of the coastal processes, sediments, hydrology, salinity, mangroves and salt marsh, and the influence of local stratigraphy on hydrology that occur along the north-western coast of Western Australia, from the Dampier Peninsula to Shark Bay, as it has direct relevance to the development and occurrence of soldier crab habitats. It helps explain the spatial variation in sediments (and hence habitats) across beaches and tidal flats, and the physico-chemical factors and processes that underpin the development of soldier crab habitats, and helps explain those locations where soldier crab habitats will not be developed. The information is derived from Davies (1970), Logan & Cebulski (1970), Logan *et al*. (1970, 1974), Brown & Woods (1974), Hagan & Logan (1974a, 1974b); Read (1974); Johnson (1982); Semeniuk (1981, 1983, 1985, 1986, 1993, 1995, 1996, 2005, 2008); Galloway (1982), Semeniuk *et al*. (1982); Thom (1982, 1984), Wright *et al*. (1982); Short & Wright (1984), and Semeniuk & Wurm (1987). The synthesis of coastal processes, sedimentology, hydrology, salinity, and local stratigraphy that follows relates to development and internal features of a given tract of coast at site-specific level (*e.g*., a pocket beach or a prograded tidal flat) but not at a scale of the evolution of integrated coastal systems such as deltas, ria shores, or barrier-island complexes (*e.g*., Semeniuk 1985, 1996, 2008).

Critical processes and products occurring and developed along the north-western coast of Western Australia involve: 1. terrestrial processes (such as the supply of terrigenous sediment); 2. local biogenic sediment production; 3. sediment types developed along the shore; 4. coastal processes (such as waves, wind, and tides) developing geomorphic units along the shore; 5. the groundwater systems; 6. tidal-zone groundwater levels; 7. tidal-zone groundwater salinity and gradients; 8. fresh-water seepage and seawater seepage; and 9. tides and the drying of the shore surface resulting in variation in pellicular water content and its salinity (*cf*. Semeniuk 1983). Many of these are inter-related, for instance, tidal range and slope of tidal shore have influence on the extent and rapidity that tidal-zone groundwater can discharge down-gradient.

Terrestrial processes, such as fluvial delivery of sediment, or sheet-wash, amongst others, result in variable supply of terrigenous sediment to the coast. This is particularly relevant in parts of the coast that receive fluvial influx (Semeniuk 1993), such as the Gascoyne River Delta (Johnson 1982), the Wooramel River Delta (Logan *et al*. 1970), and the Pilbara Coast deltas (Semeniuk 1995). While terrestrial processes deliver silicic sand to the coast to form deltas and other coastal sand deposits, of particular importance also is the supply of terrigenous mud which accumulates in the shore zone in the mid- to upper-tidal level (Semeniuk 1993, 2005). Biogenic sediments also accumulate at the coast as gravel-, sand-, and mud-sized skeletons and fragments. Additionally, calcium carbonate mud may be deposited along the shore by the breakdown of calcareous biota, or by influx from offshore. Coastal processes involving waves, wind, and tides erode, mobilise, shape and help accumulate these sediments as shell and lithoclast gravel, silicic sand, calcium carbonate sand, calcareous quartz sand, muddy sand, and terrigenous mud and calcium carbonate mud, in various geomorphic settings and sedimentary environments such as tidal flats, beaches, coastal dunes, spits, and cheniers, amongst others. With adequate supply of materials, sediments prograde to develop coastal muddy plains, muddy plains punctuated by stranded barriers and beachridges, sandy beachridge plains, accreted spits, cheniers, and dunes (Semeniuk 1993, 2008).

Setting aside rocky shores which, axiomatically, are largely sediment-free and thus are not soldier crab habitats, the accretionary sedimentary coastal systems of the north-western coast of Western Australia can be divided into three end-members, which can be related to the extent that wave energy impacts on the shore and the amount of sediment supplied to the coast: 1. sand-dominated, 2. sand-and-mud systems, and 3. mud-dominated.

Within a framework where wave energy influences the type of sediment that accumulates along the shore (with the caveat that sediment supply can determine whether sediments accumulate even in extremely high-energy environments), a simplified diagram that relates sedimentary coastal forms to wave energy, from the highest energy to the lowest energy is presented in Figure 5A. In terms of wave energy, at one extreme, sand-dominated systems tend to be wave-dominated systems, while mud-dominated systems tend to be areas with low wave energy. Within this spectral framework, soldier crab habitats are located in sand-dominated systems (but which do not experience the highest wave energy impinging on the shore), or within sand-and-mud systems. In Western Australia, mud-dominated systems are not sites for habitats for *M. occidentalis*, and as such are not considered further here.

The sand-dominated systems generally occur in prograded beachridge plains, sand-dominated deltas, barrier-dune coasts, coastal sand ribbons, or pocket beaches (often between headlands). Examples of sand-dominated shores are the beach-dune shores of the Peron Peninsula in Shark Bay, the beach-dune tract at and near Onslow on the Pilbara Coast, and Eighty Mile Beach along the Canning Coast. If soldier crab habitats are to occur within these sand-dominated systems, they are located where there is some specific relative protection from waves (*e.g*., in the lee of local rocky reefs on a beach, such as at Entrance Point, Broome), leeward of locally-developed, low-relief shoals (*e.g*., Settlers Beach near Cossack), behind low-relief, beach-ridge barriers or in the most sheltered part of a cove, protected from swell and wind waves by its orientation (*e.g*., northern Hearsons Cove in the Dampier Archipelago), or where wave dampening occurs because of low gradients in the shore face, *i.e*., dissipative shores, such as along the tract of Eighty Mile Beach. High energy in wave-dominated systems involves extensive daily reworking of the sand substrate to depths of 10–30 cm, generating megaripples or plane beds (Reineck & Singh 1980; Shipp 1984), both resulting in marked mobility of sand in the depth interval where soldier crabs would normally reside. Thus, in sand-dominated sedimentary systems the occurrence of soldier crab habitats will depend on the level of wave energy impinging on the shore, the extent the shore is wave-dissipative, and what degree of shelter or degree of wave dampening can be developed by local factors or features in the environment (such as rocky headlands, spits, and shore-parallel shoals and depressions).

Sandy environments in extreme macrotidal settings also are subject to strong tidal reworking, with development of megaripples and plane beds (see Figure 3 of Semeniuk 1981), again, resulting in marked mobility of sand in the depth interval where soldier crabs would normally reside.

Sand-and-mud-dominated systems occur in many locations along the north-western coast of Western Australia. Where there is the occurrence of both sand

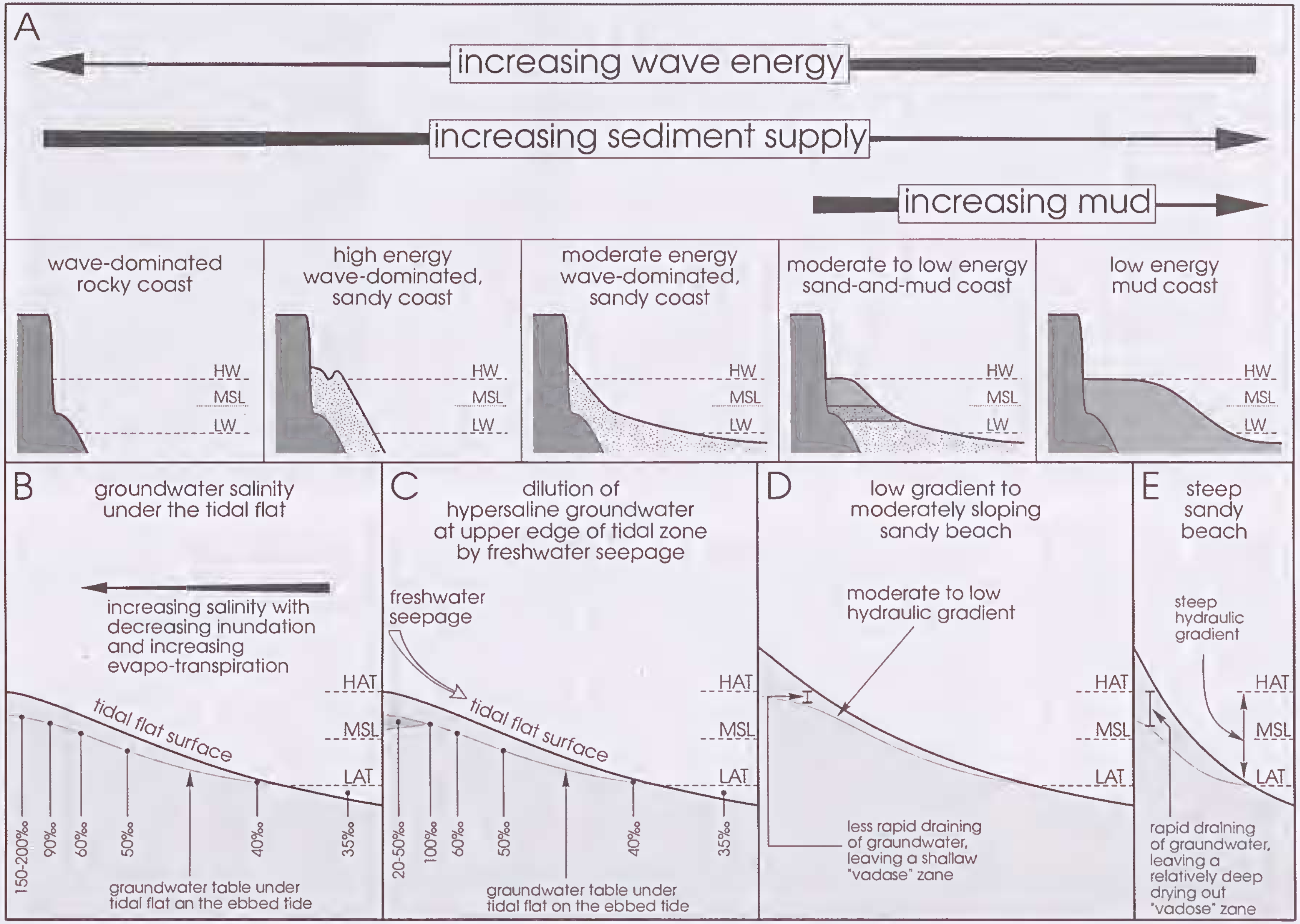


Figure 5. Various physical settings that determine soldier crab habitats. A. Simplified diagram that relates sedimentary coastal forms to wave energy – from the highest energy to the lowest energy, resulting in rocky shores at one extreme, to sandy and sand-and-mud coasts in intermediate settings to mud-dominated coast at the other extreme. B and C. Groundwater salinity increasing along the tidal gradient from LAT to HAT, and the dilution effect of seepage of freshwater. D. Draining of phreatic water during low tide on a moderately sloping to low-gradient sandy beach resulting in shallow vadose zone. E. Draining of phreatic water during low tide on a more steeply sloping sandy beach resulting in relatively deeper vadose zone.

and mud on a tidal flat in tide-dominated systems (such as King Sound), sand will accumulate in the lower end of the tidal range, which also is the most inundated and subject to more prolonged wave reworking, while mud accumulates in the mid- to upper-tidal zones, which also is the zone progressively the least inundated and subject to less prolonged wave reworking (Semeniuk 1981, 2005). Mud accumulates in the upper-tidal zones because of the phenomenon of scour-lag and settling-lag (Postma 1967). Where there is both sand and mud in wave-dominated systems, and where there is partitioning of the shore into a reflective beach and a dissipative shore, sand will accumulate in the upper end of the tidal range, and mud will tend to accumulate in the low tidal and subtidal environments.

The zone of transition along the tidal gradient between accumulations dominantly of sand and those dominantly of mud will be inter-layered sand and mud, or burrow-mixed muddy sand (Semeniuk 1981, 2005). Depending on the ratio of sand to mud in a given location, the boundary between the sand-dominated and mud-dominated facies can occur anywhere from the level of LWN to MSL: in King Sound it is at ~ MLWN, at King Bay it is mid-way between MSL and MLWN, and at Withnell Bay it is at ~ MSL. As will be shown later, soldier crab occurrence is related to content of mud in the sediment, and the occurrence of soldier crabs in sand-to-mud facies will be related to the boundary condition between sand and mud, and in particular where mud comprises only a low proportion of the muddy sand. In other words, where mud begins to accumulate on the tidal slope, a specific content of mud in the sandy sediment can determine where along the tidal gradient the soldier crab will be eliminated.

In terms of groundwater residing under tidal sediments, the coastal zones where soldier crabs occur are influenced by two groundwater systems (Semeniuk 1983, 1985; Semeniuk & Wurm 1987): (1) marine water which inundates the tidal flats daily, and recharges the groundwater system under the tidal flat and under beaches; and (2) fresh water residing in the hinterland which discharges into the tidal zone along specific conduits or along an interface. With daily inundation between MSL and low tide, the salinity of the groundwater and pellicular water under the tidal flat tends to approximate that of the recharging marine waters (*i.e.*, ~ 35–40 ppt). Higher along the tidal gradient, with less frequent flooding and more exposure to solar-induced evaporation, transpiration, and wind-induced evaporation, the salinity of groundwater and pellicular water progressively increases (Semeniuk 1983, 1985; Semeniuk & Wurm 1987). On tidal flats at the edge of the landward mangroves, for instance, at levels ~ MHWS, salinity of groundwater is ~ 90 ppt, and towards the edge of the salt flats at levels of highest spring tides, depending on tidal range and on climate, it may reach 150–180 ppt (Semeniuk 1983). Thus, there is a gradient of increasing salinity of groundwater and pellicular water from near-marine on the low-tidal flats to 150–180 ppt on the high tidal flat, in response to decrease in marine recharge and increase in evaporation and transpiration. This gradient is complicated where there is delivery of fresh water or seawater into hypersaline groundwater by appropriate aquifers.

Fresh water discharging into the tidal environment, particularly along the interface of the hinterland and the level of the highest tide, dilutes any hypersaline groundwater and pellicular water that might normally have been present in high-tidal zones, reducing their values to as low as ~ 27 ppt. Seawater invading appropriate sedimentary aquifers (such as the margin of a sandy dune, or high-tidal beach sand wedges) during a high tide also can discharge downslope on an ebb tide, delivering seawater by seepage to tidal zones whose groundwater and pellicular water normally might be hypersaline. Apart from their influence on groundwater and pellicular water salinity, fresh-water seepage and seawater seepage also have the effect of increasing moisture content in the surface sediments. This is particularly important in high-tidal areas that would normally be relatively dry and saline during the low tide or neap tide. For seawater seepage, it is significant in mid-tidal areas where steep (reflective) beaches or moderately sloping beaches interface with low-gradient tidal flats (or dissipative shores); seawater discharges from the base of the beach onto the lower tidal flat (Figure 6). This hydrological situation is ubiquitous along

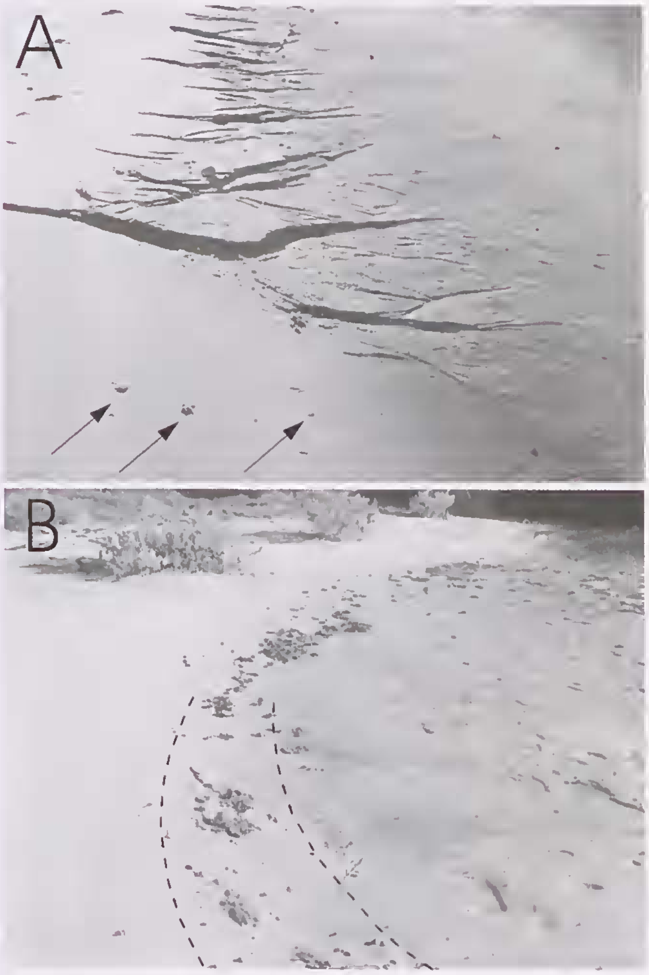


Figure 6. Seepage of seawater on an ebb tide from the base of a beach slope on a reflective beach. A. Strong seepage at Six-mile Creek East (occurrences of soldier crab pustules are arrowed). B. Moderate seepage at Mangrove Bay (upper and lower margin of the zone of soldier crab workings is outlined). This seepage is located along the junction of sand (of the beach) and slightly muddy sand (of the tidal flat).

the shores of north-western Australia where reflective beaches interface with dissipative shores, and it is important in the development of local soldier crab habitats.

There are various stratigraphic settings and interfaces that have an important function in the hydrology of tidal flats, and seepage, as described above, is especially pronounced where there are appropriate stratigraphic contacts and unconformity surfaces. For example, the discharge of seawater or fresh water, from sand along a sand/mud interface can be a locally important site for the development of soldier crab habitats. Similarly, seawater or fresh water, stored in a sand aquifer that discharges along a relatively impermeable or less permeable interface (such as an unconformity cut on limestone), also can result in the local development of habitats for soldier crabs. Various settings for storage and discharge of seawater or fresh water, where they result in soldier crab habitats, are shown in Figure 7.

An important component of the tidal-flat hydrology is the level of the groundwater table under the tidal flat or beach during the low tide. When the tide has ebbed, the levels of groundwater under the tidal flat, or the beach, descend. This results in water-saturated sediment becoming undersaturated (marine phreatic water becomes marine pellicular water). Over an ebb-tidal period, on a relatively moderately sloping mid-tidal flat underlain by sand, the water table can drop 30–80 (–100) cm. On a relatively low-gradient mid-tidal flat, underlain by sand, the water table may drop only 10–20 cm. Once exposed by an ebb tide, the tidal-flat surface and the pellicular water therein are subjected to solar radiation and wind, resulting in a drying of the surface, and an increase in pellicular water salinity.

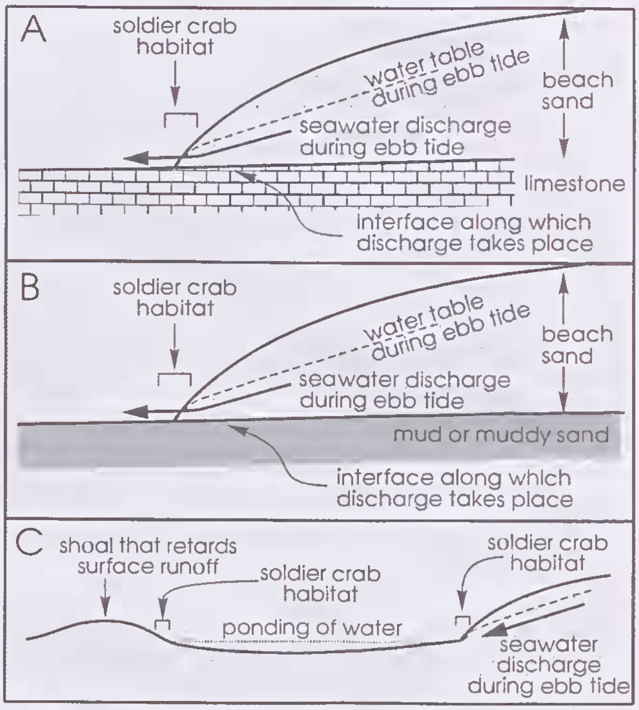


Figure 7. The influence of stratigraphy on tidal flat hydrology and the development of soldier crab habitat at the base of beach slopes. A and B. Seepage of seawater (discharge of groundwater) during ebb tide with discharge located along a stratigraphic interface – an unconformity cut into limestone for (A) and a mud or muddy-sand layer (for B). C. Discharge of seawater at the base of a beach slope developing a soldier crab habitat. Also, shoal acts as a "dam" retarding seawater discharge on an ebb tide, resulting in longer moisture retention on the landward margin of the shoal and hence development of a soldier crab habitat.

The extent to which the surface dries, the water table falls below the tidal flat, and the salinity of the pellicular water increases over the ebb-tide period will depend on a number of factors: 1. the tidal range (large tidal ranges provide more scope for larger groundwater table drop because of the larger hydraulic head between the groundwater level and the low-tide level); 2. the slope of the surface (the steeper surfaces will drain groundwater more rapidly, leaving a greater thickness of pellicular water); 3. the position on the tidal gradient (LWN levels and the mid-tidal level will drain more completely, respectively, than LWS levels, firstly because of the increasing hydraulic head upslope on the tidal flat, secondly because the lower tidal levels would not have enough hydraulic head to fully complete draining, and thirdly because there would not be enough time to fully drain low-tidal parts of the tidal flat before the return of the flood tide); and 4. sediment type (sand will drain more rapidly than muddy sand and mud). Figures 5B–5E summarise these aspects of the environment. Some features of the dynamics of groundwater table, recharge and discharge, and capillary fringe effects on beaches have been described and discussed by Emery & Foster (1948), Erickson (1970), Lanyon *et al.* (1982) and Turner (1993); the reader is referred to these works for some background information. In this paper, we focus on the effects of hydrologic patterns on the beach and sandy shores in generating and maintaining soldier crab habitats.

In response to tidal inundation, groundwater and pellicular water salinity, sediment types, and biological factors (such as inter-species competition), mangroves and salt marsh may inhabit particular levels of the mid- to upper-tidal zone. Mangroves occur between ~ MSL and ~ MHWS, in zoned floristic assemblages and zoned structural forms (Semeniuk *et al.* 1978; Semeniuk 1983, 1985, 1993; Semeniuk & Wurm 1987). Mangroves can inhabit mud-dominated substrates, muddy sand substrates, and sand-dominated substrates. In the realm of the Western Australian soldier crab, mangroves inhabiting sand-dominated substrates are important, because they reside in niches the soldier crab could have occupied. Salt marsh, and in particular, *Sporobolus virginicus* (the sea couch) occurs at level of ~ HAT or MHWS, tending to inhabit the high-tide zone in sandy environments. Both are mentioned here because they have an influence, at the local scale, on the occurrence of soldier crabs in north-western Australia.

Results

Regional distribution of soldier crabs

Along the Western Australian coast, soldier crabs occur in a wide range of coastal settings (each setting with its specific wave energy), tidal environments, gradients of tidal flats, (sandy) sediment types, and environments with or without cover of mangroves or sea couch. Soldier crab occurrences as presence/absence based on the 1980–2008 surveys, and long-term records of the Western Australian Museum, dating back to 1939, are noted in Table 5 and Figure 8, and described in Appendix 1. Brief descriptions of the coast along Western Australia where surveys for soldier crabs were undertaken also are provided in Appendix 1.

In the ensuing text on the regional distribution of soldier crabs, the northern and southern limits of the biogeographic distribution of *M. occidentalis* are described first. The environmental information for the northern and southern limits of the species is derived from Semeniuk (1981) for King Sound, from Davies (1970), Logan & Cebulski (1970), Logan *et al.* (1970), Brown & Woods (1974), Hagan & Logan (1974a, 1974b) and Read (1974) for Shark Bay, as well as more site-specific data obtained during this study as presented in Appendix 1.

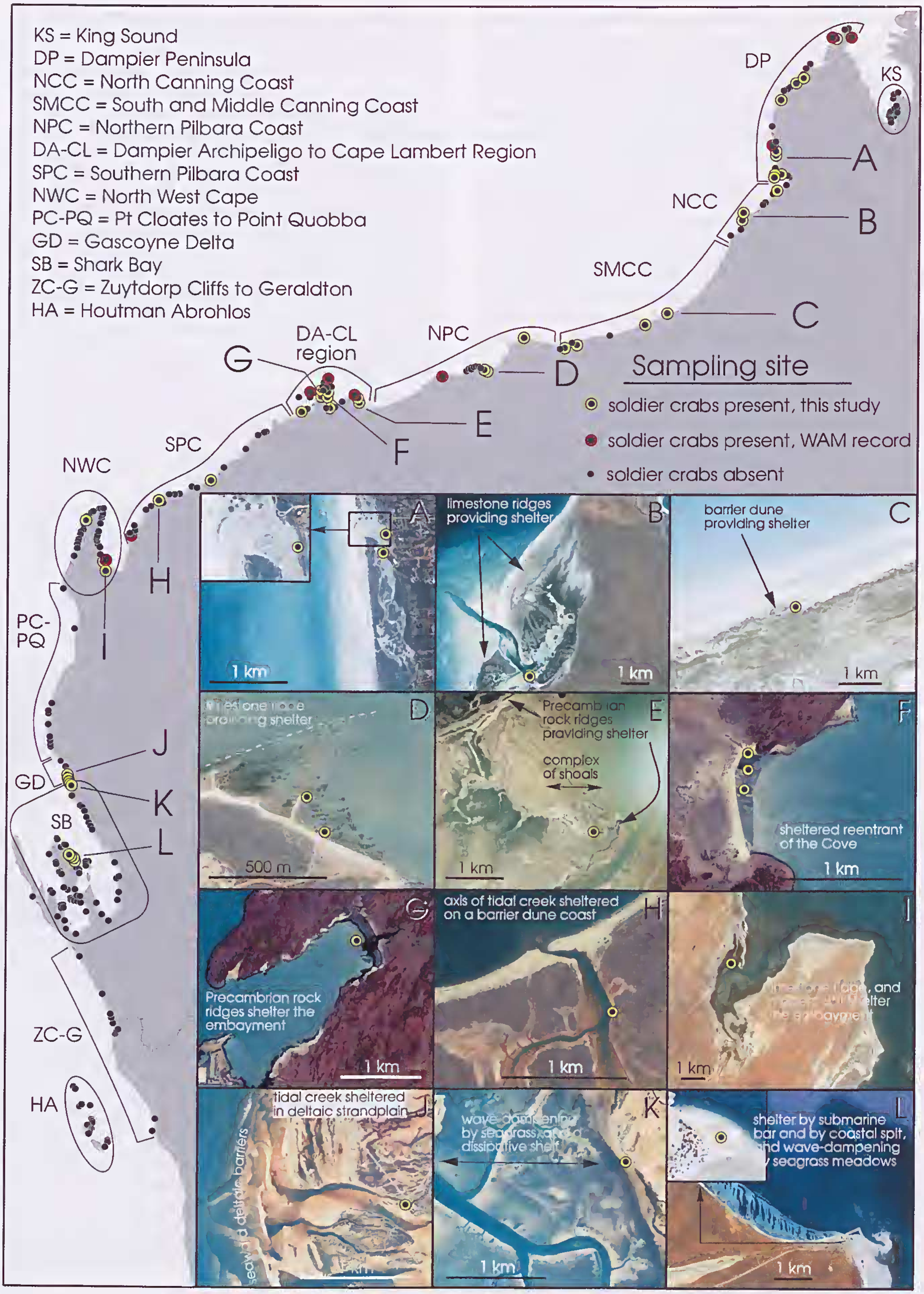
The northern boundary of the distribution of *M. occidentalis* is One Arm Point, east of Cape Leveque, essentially the north-western extremity of King Sound (Figure 8). *M. occidentalis* has not been recorded in the interior of King Sound (Semeniuk 1981). The gulf of King Sound is an extreme macrotidal, sand-and-mud sedimentary system wherein there are three sedimentary environments (Semeniuk 1981): 1. mud accumulating at tidal levels from ~ MSL to HAT, and obviously providing no soldier crab habitats; 2. an abundance of mud mixed with varying amounts of sand that accumulates at tidal levels from ~ MLWN to MSL (progressing from MLWN, this accumulates as muddy sand, or interlayered sand and mud), and obviously not providing soldier crab habitats; and 3. high-energy, low-tidal sand flats that are megarippled and physically reworked daily to depths of 10–30 cm during spring tides, and dominated by the sand bubbler crab (this also is not a soldier crab habitat).

The southern limit of the range of the species is in the Monkey Mia area (5 sites), with the crab inhabiting a sand-floored lagoon leeward of a spit at Monkey Mia, and shoal-and-depression sand flats about 5 km north and south of Monkey Mia. Surveys within Shark Bay into other possible occurrences of soldier crabs outside of the Monkey Mia location, involving 67 additional habitat-specific sites, failed to find the species, though locally there were appropriate tidally-exposed sand flats and sand shoals. Much of Shark Bay is too wave agitated to support soldier crabs. For instance, the east coasts of Hopeless Reach, Disappointment Reach, and Freycinet Reach are subject to strong southerly winds (Logan & Cebulski 1970) and their derivative wind waves. The southerly derived wind waves intersect the NNW-trending coasts of Hopeless Reach, Disappointment Reach, and Freycinet Reach, developing active north-trending spits, emanating from promontories. Sediment along the seaward margins of the spits is too mobile and too coarse for soldier crabs. Sheltered environments leeward of the spits tend to be muddy (with mud derived from the nearby seagrass banks; *cf.* Davies 1970). In this context, of particular significance is the absence of soldier crabs along the east coast of Hopeless Reach south of Gascoyne Flats (Transect Site 24 of this study): soldier crabs occur along the Gascoyne Flats on the northern side of the Boodalia Delta, a location that is sheltered from southerly winds and wind waves by the protruding lobe of this Pleistocene delta (Logan 1974; Johnson 1982), but not along the remainder of the eastern coast of Hopeless Reach southwards. Elsewhere in Shark Bay, currents and wave action have resulted in many of the tidal flats, where soldier crabs might be expected, being winnowed to form shell pavements. In other locations in Shark Bay, low gradient, poorly draining tidal flats (*i.e.*, without shoal-and-depression systems) are too water-saturated (too wet) at low tide (*i.e.*, groundwater at low tide is at the sediment surface), and unsuitable for soldier crabs. Towards the southern parts of the Shark Bay system, the open waters become progressively more saline, particularly in Hamelin Pool where they are hypersaline (Logan & Cebulski 1970; Hagan & Logan 1974a; Read 1974). The trend in increasing salinity is augmented further in the shallow waters and tidal zone of the southern Shark Bay inlets, and reflected in the occurrence of algal mats and breccia pavements in the environments where soldier crabs might have been expected.

Surveys outside of Shark Bay into possible occurrences of soldier crabs failed to find the species, though locally there were appropriate tidally-exposed sand flats and sand shoals. Critical areas were the sand flats and sand shoals within the estuary of the Murchison River at Kalbarri, the sand flats at Geraldton (latitudinally opposite Houtman Abrolhos), and the island margins and embayments in the Houtman Abrolhos. *M. occidentalis* was not found on the tidal sand flats and sand shoals in the Murchison River estuary, nor at Geraldton.

The margins of the islands in the Houtman Abrolhos were dominated by limestone cliffs, limestone pavements, coral-gravel shores, or high-energy, pocket sandy beaches, all of which are not soldier crab habitats. Most of the relatively low energy mangrove-lined embayments in the reef-and-island complex were underlain by limestone pavement, sand veneer on limestone pavement, or coral gravel; these also were not soldier crab habitats. The most sheltered sites, locally lined by mangroves at MSL, and that were underlain by tidally-exposed sand flats, were inhabited by dense populations of sand-tube worms. Thus, most of the twenty-four sites examined as the most likely location for *M. occidentalis* (sites HA-1 to HA-24 in Appendix 1) were not soldier crab habitats, and the species did not occur on any of the tidally-exposed, sheltered sand flats examined in the reef-and-island complex. Dakin (1919) and Montgomery (1931) in their extensive surveys and studies of marine fauna of the Houtman Abrolhos also did not record *Mictyris* in the islands.

Within the biogeographic range of *M. occidentalis*, where soldier crabs do occur along the coast (Figure 8), they are in embayments, along sandy tidal-creek banks, within lagoons within the strand plain of deltas, within lagoons behind barriers (be they high-relief or low-relief), in the indented coasts of ria/archipelago systems, along sandy beach coasts where local factors combine to provide relative shelter, and along sandy coasts that are low-gradient and energy-dissipative. Figure 8, in presenting information on the occurrence or absence of soldier crabs, provides an indication of the patchy extent along the coast and the type of habitat settings that *M. occidentalis* can occupy. The aerial photographic insets are of locations where the species was found in this


KS = King Sound
DP = Dampier Peninsula
NCC = North Canning Coast
SMCC = South and Middle Canning Coast
NPC = Northern Pilbara Coast
DA-CL = Dampier Archipeligo to Cape Lambert Region
SPC = Southern Pilbara Coast
NWC = North West Cape
PC-PQ = Pt Cloates to Point Quobba
GD = Gascoyne Delta
SB = Shark Bay
ZC-G = Zuytdorp Cliffs to Geraldton
HA = Houtman Abrohlos
KS
DP
A
NCC
B
SMCC
C
NPC
DA-CL region
G
D
E
F
SPC
NWC
H
I
PC-PQ
J
GD
K
SB
L
ZC-G
HA
Sampling site
soldier crabs present, this study
soldier crabs present, WAM record
soldier crabs absent
A
1 km
limestone ridges providing shelter
B
1 km
barrier dune providing shelter
C
1 km
limestone ridge providing shelter
D
500 m
Precambrian rock ridges providing shelter
E
complex of shoals
1 km
F
sheltered reentrant of the Cove
1 km
G
Precambrian rock ridges shelter the embayment
1 km
axis of tidal creek sheltered on a barrier dune coast
H
1 km
I
limestone ridges, and ... shelter the embayment
1 km
tidal creek sheltered in deltaic strandplain
J
seaward deltaic barriers
1 km
wave-dampening by seagrass and a dissipative shelf
K
1 km
shelter by submarine bar and by coastal spit, and wave-dampening seagrass meadows
L
1 km

study, and illustrate the variety of coastal settings in which habitats occur, though not all the sites form the basis for the detailed twenty-five study transects. The range of features evident in the photographic insets of Figure 8 for the various coastal sectors of north-western Australia is described below.

Figure 8A shows a soldier crab habitat along the Canning Coast at Coconut Well in a tidal lagoon protected by a sand barrier. Figure 8B shows a soldier crab habitat along the Canning Coast at Port Smith in a tidal-creek complex behind a limestone barrier. Figure 8C shows a soldier crab habitat along the Canning Coast at Mandora in a shore-parallel, tidal-creek system sheltered by a sand barrier. Figure 8D shows soldier crab habitats at the base of a reflective beach (the eastern site), and within a dissipative shore (the western site), both sheltered by a Pleistocene limestone ridge, near Port Hedland along the Pilbara Coast. Figure 8E shows a soldier crab habitat in a shoal complex within an embayment partially sheltered by Precambrian rock ridges, near Cossack along the Pilbara Coast. Figure 8F shows soldier crab habitats in the sheltered re-entrant of Hearsons Cove, protected by Precambrian rock ridges; the soldier crab habitats occur in a shoal complex on a dissipative sandy shore, and on a high-tidal, sandy alluvial fan. Figure 8G at Withnell Bay shows a soldier crab habitat in a deeply indented embayment sheltered by Precambrian rock ridges, the length of the embayment being a dissipative slope. Figure 8H shows a soldier crab habitat along the axis of a tidal creek near Onslow along the Pilbara Coast; the open coast is a high-energy sandy shore. Figure 8I shows a soldier crab habitat on the low-tidal sand flats in the interior of a V-shaped embayment bordered and partly sheltered by limestone ridges in the Little Bay of Rest, southern Exmouth Gulf. Figure 8J shows a soldier crab habitat along a tidal-creek bank on the strand plain of the Gascoyne Delta; the open barrier coast is high energy. Figure 8K shows a soldier crab habitat developed along the upper tidal zone of the Gascoyne Flats of the Wooramel Seagrass Bank, north-eastern Shark Bay; the shore is protected from Indian Ocean swell by Dorre Island and, locally, the seagrass bank has dampened wave action. Figure 8L shows a soldier crab habitat developed along a sandy shore at Monkey Mia; the site is a sand-floored lagoon, partly protected by a large, seagrass-vegetated submarine spit, partly sheltered by the dampening of wave action by seagrass meadows, and protected by a local recurved shoreline spit.

The various settings for all known occurrences of soldier crabs recorded thus far in Western Australia, based on this study and Western Australian Museum records, as shown in Figure 8 are briefly described in Table 5. More specific features for some of the habitats are described in the twenty-five transects at the specific study sites Tables 6 and 7.

Figure 8 and Appendix 1 show that the coast between One Arm Point and the Monkey Mia area provides a variety of discrete and discontinuous occurrences of soldier crab habitats and soldier crab populations. They also show that there are *extensive* tracts where soldier crab habitats are absent – this is because cliffed (rocky) shores, or the high-energy beach/dune shores dominate the coast.

The cliff coast along the western margin of Edel Land (Logan *et al.* 1970) is the best example of cliffed (rocky) shores. The coast of Edel Land is latitudinally and climatically equivalent to the Monkey Mia area (where soldier crabs do occur), but is comprised of Quaternary limestone, and without offshore reefs, it is subject to swell and wind waves. The coast is strongly eroded, resulting in high cliffs. To the south, the Zuytdorp Cliffs and the limestone cliffs and pocket beaches extending to the cliff coast of Kalbarri (*i.e.*, Red Bluff), present another tract of coast that is wave-dominated with high-cliffs which would not develop soldier crab habitats. Proceeding northwards from Monkey Mia, the coast between Point Quobba and Vlamingh Head, cut into Tertiary limestones and Quaternary limestones, is similar geomorphically to Edel Land and the Zuytdorp Cliffs, but while comprised dominantly of cliffs, there are local ribbons of shoreline sand. Wave energy is still too high for soldier crab habitats. Along the northern part of the Canning Coast, leaving aside small sheltered embayments such as Willie Creek and Coconut Well, the west coast of the Dampier Peninsula, between Broome and Cape Leveque, is a wave-dominated, cliffed rocky shore, cut into Mesozoic and Quaternary rocks, semi-indurated dunes, and stretches of high-energy beaches (Gibson 1983a, 1983b; Semeniuk 2008) – soldier crab habitats are not developed.

Along all these tracts of extensive cliff coasts, there may be very localised small pocket beaches, embayments, or ravine re-entrants (*e.g.*, Yardie Creek on the west coast of North West Cape) where soldier crabs potentially *may* occur, but generally the coastal tracts are too high-energy and too rocky to favour development of such habitats. For instance, of thirty sites along the eastern and western sides of North West Cape, soldier crabs were found only at five very protected embayments within the region.

Hence, in the dominantly rocky tracts between Red Bluff (Kalbarri) and Vlamingh Head, and the west coast of the Dampier Peninsula, the rocky shores, or the high energy conditions are laterally extensive along the coast, and there is a general absence of soldier crabs.

The Pilbara Coast presents a somewhat different situation for rocky shores and cliff coasts to that described above, in that the coastal tract is relatively more heterogeneous at the megascale, mesoscale, and microscale (Semeniuk *et al.* 1982; Semeniuk 1985; Semeniuk & Wurm 1987; Semeniuk 1996), and the high-

◀ **Figure 8.** Map of sampling sites in Western Australia, absence or presence of soldier crabs, and location of aerial photographic insets. Description of the insets A–L of aerial photographs of soldier crab occurrences is provided in the text. Various parts of the coast are subdivided into tracts, and sites within these tracts are numbered as listed and described in Appendix 1. While all 316 sites are not clearly visible at the scale of this illustration, the reader can locate individual sites – when they are spatially closely located – from their latitude/longitude co-ordinates presented in Appendix 1. However, the recorded occurrences of soldier crabs along the coast are clearly evident as indicated by the yellow- or red-coloured circles with black centres.

Table 5

Occurrences of *M. occidentalis* along the Western Australian coast based on the 1980–2008 surveys (this study) and Western Australian Museum (WAM) records (geographic locations shown in Figure 2). Asterisk indicates that the location is one of the twenty-five transect study sites of this paper.

Site	Source	Description of site(s)
One Arm Point	WAM	sand shoals at ~ LWN
Lombadina	WAM	sand shoals at ~ LWN in embayment
Beagle Bay	this study	sand shoals in axis of tidal creek at ~ LWN
Camp Inlet	this study	sand shoals in axis of tidal creek at ~ LWN
Barred Creek	WAM	sand shoals in axis of tidal creek at ~ LWN
Willie Creek area	this study	(1) sand shoals of ebb tidal delta at ~ MLWN-MSL; (2) partly barred lagoon at ~ LWN; (3) a shoal-and-depression complex between MSL and ~ LWN
Coconut Well *	this study	(1) tidal lagoon at MHWS; (2) ~ HAT margin of dune
junction of Gantheaume Point with southernmost Cable Beach	this study	sand flat between MSL and MLWN leeward of rocky reefs
Entrance Point *	this study	sandy beach between MSL and MLWN between two rocky peninsula
north of Broome Port	this study	sand flats between MHWN and MLWN seaward of mangrove copses and in sand patches between mangrove copses
Broome Town foreshore *	WAM/this study	MHWS sand flat landward of mangroves
Black Ledge	this study	pockets of sand ~ MSL between outcrops of sandstone
Thangoo	this study	sand flat ~ MSL, seaward edge and immediately seaward of mangroves
Thangoo south	this study	sand flat ~ MSL, seaward edge and immediately seaward of mangroves
Port Smith	this study	sand flat between MSL and MLWN in axis of tidal creek
Cowan Creek (NE)	this study	sand flat between MSL and MLWN
Mandora	this study	sand shoals MSL-MLWN in tidal creek behind sand barrier
Eighty Mile Beach	this study	sand flat between MSL and MLWN
De Grey River Delta	this study	sand shoals MSL-MLWN in sheltered mouth of delta
Nine-mile Creek *	this study	sand flat at MHWS within mangroves
Six-mile Creek East *	this study	base of beach slope at ~ MSL
Six-mile Creek West *	this study	sand flat at MSL-MLWN
Mundabullungana	WAM	sand shoals in axis and mouth of large tidal creek
Cape Keraudren area	this study	(1) sand flat at MSL-MLWN; mid-channel creek shoals of Cootenbrand Creek at ~ MHWN; (2) sand floor of fringing mangrove copse between MSL and MHWN; and (3) sandy bank of Mosquito Creek at MHWN
Red Bluff, northeast of Pardoo	this study	sand flat and beach at MSL-MLWN
Cossack (East) *	this study	sand flats at MSL-MLWN
Settlers Beach *	this study	base of beach slope at ~ MSL and sand shoals MSL-MLWN
Point Samson *	this study	base of beach slope at ~ MSL and sand shoals MSL-MLWN
Mko Bay (sic)	WAM	sand shoals in axis of dune-barred tidal creek
Hearsons Cove area*	this study	(1) sand shoals at MSL-MLWN; (2) alluvial fan at MHWS
Nickol River	this study	sand shoals at MSL-MLWN at entrance to Nickol River
Conzinc Bay *	this study	sand flat at MSL-MLWN
Withnell Bay *	this study	sand flat at MSL-MLWN
West Lewis Island	WAM	sand flat at MSL-MLWN
Tozer Island	WAM	sand flat at MSL-MLWN
King Bay area *	this study	(1) sand flat and shoals at MSL-MLWN; (2) shoal in axis of tidal creek
Maitland River Delta	this study	sand flats ~ MSL in lagoon on delta front
Onslow *	this study	mid-tidal sandy bank of tidal creek
Simpson Island NE	this study	sand flat leeward of island at MSL-MLWN
Simpson Island SE	WAM	sand flat in axis of tidal creek complex
Bay of Rest	WAM/this study	sand shoals in protected embayment, MSL-MLWN
Little Bay of Rest	this study	sand shoals in protected embayment, MSL-MLWN
Mangrove Bay *	this study	base of beach slope at ~ MSL in protected embayment
One Tree Point *	this study	point bar on tidal creek on strand plain
Babbage Island area *	this study	(1) point bar on tidal creek, (2) sand flat of tidal lagoon on strand plain
The Fascine, Gascoyne Delta	this study	sand shoals ~ MSL within delta channel
Mangrove Point, Gascoyne Delta	this study	sand flat ~ MSL within and immediately seaward of mangroves
Gascoyne Flats, NW Shark Bay *	this study	mid-tidal edge of seagrass-vegetated flat (Wooramel Seagrass Bank)
Cape Rose, Shark Bay	this study	mid-tidal sand flat in a shoal-and-depression complex
Red Cliff, Shark Bay	this study	mid-tidal sand flat in a shoal-and-depression complex
Monkey Mia, Shark Bay *	WAM/this study	mid-tidal sand flat behind shoreline spit, sheltered by a submarine spit
south of Monkey Mia, Shark Bay	this study	mid-tidal sand flat in a shoal-and-depression complex
north of Dubaut Creek, Shark Bay	this study	mid-tidal sand flat in a shoal-and-depression complex

energy coastal forms are not as laterally extensive as described above. The megascale coastal types such as deltas, beach/dune coasts, embayment coasts, ria/archipelago coasts, and limestone barriers alternate in occurrence in this region. Within these, there is a range of smaller-scale coastal forms, from rocky shores, to wave-dominated sandy coasts, to sheltered embayments, that occur in discrete localised areas (Semeniuk 1996). Thus there are stretches of rocky shores and cliff coasts along the Pilbara Coast (*e.g.*, along the seaward edge of limestone barrier coasts, and along rocky shore tracts of ria/archipelago coasts) and, although of high energy, they are of relative low relief compared to the wave-dominated cliff coasts described earlier. Nonetheless, as wave-dominated rocky coasts, they do not provide soldier crab habitats. On the other hand, the localised embayments, lagoons, or tidal creeks developed in relative shelter, do provide soldier crab habitats. Hence, soldier crab habitats and soldier crab-free zones occur in patches along the Pilbara Coast corresponding to sheltered zones alternating with (strongly) wave-exposed zones.

The open coast of the Gascoyne Delta, beach/dune coasts along the Onslow tract, the sea-front of many of the wave-dominated deltas of the Pilbara Coast, and local tracts of the Canning Coast are good examples of the effects of high wave energy along sandy coasts. The Gascoyne Delta is wave-dominated (Galloway 1975; Coleman 1976; Reineck & Singh 1980; Johnson 1982), receiving swell and wind waves. The front of the delta is dominated by mobile, rippled and megarippled sand (Johnson 1982), and there are no soldier crabs in the tidal zone. Soldier crabs do occur in the Gascoyne Delta but in the tidal lagoons and creeks that are sheltered by barrier dunes or barrier beach ridges that frame the seafront and interior of the stranded interior of the delta. The beach/dune shores and the sea-front of the wave-dominated deltas of the Pilbara Coast, exemplified by the Onslow tract and Ashburton Delta, are further examples of wave-dominated systems, which are too high-energy, and the sand too mobile for the development of soldier crab habitats. This is a similar situation for tracts of the Canning Coast (Semeniuk 2008): local beaches such as at Shoonta Hill, Cape Bossut, in the Cape Gourdon area, and Cable Beach are exposed high-energy, wave-dominated forms, hence soldier crab habitats are not developed on such coasts.

Transect study sites

The local habitat settings for *M. occidentalis* are described in geographical order from north to south in Table 6 for the twenty-five transect sites in terms of coastal setting, wave-energy, the habitat (geomorphic unit), the tidal level at which the crabs occur, the frequency of tidal flooding that the habitat experiences, the extent of the soldier crab zone, any key surrounding microtopography or other features, and, if applicable, descriptions of the underlying factors that support the soldier crab habitats.

The information in Table 6 shows that *M. occidentalis* can inhabit many different tidal environments, in a wide variety of tidal ranges (from microtidal to extremely macrotidal). In terms of habitats, they occupy varying tidal levels and habitat types: along open, relatively low-energy beaches with low gradients, on low-tidal sand flats, on low-tidal sand flats dominated by low-relief shoals, on sand waves, on high-tidal sand flats, on sandy banks of tidal creeks, along the margins of dunes where inundated by high tide (and where there is fresh-water seepage), within barred high-tidal, sand-floored lagoons, within those mangrove zones with sand substrates, behind mangrove zones on high-tidal sand flats, and across the sandy strand plains of deltas. The frequency of tidal flooding of their habitats can range from 3.8% to 67%.

In terms of habitats along the Western Australian coast, there are ten small- to medium-scale geomorphic units that function as soldier crab habitats and, in order of abundance, these are: 1. shore-parallel, mid- to low-tidal sand shoals and, less commonly, shore-normal, mid- to low-tidal sand shoals; 2. low topographic depression leeward of a shoal or bar; 3. mid- to low-tidal sand flats on tidal flats; 4. tidal-creek, mid-channel shoals; 5. tidal-creek banks; 6. high-tidal sand flats; 7. tidal-creek, ebb-tidal delta shoals; 8. tidal-creek point bars; 9. mid-tidal base of beach slope; and 10. high-tidal dune slope. Tidal creeks were the most heterogeneous habitat sites in having more smaller-scale geomorphic units that provide soldier crab habitat.

While the majority of localities had only one type of local-scale geomorphic unit (or habitat) supporting the soldier crab, some had a variety of habitats. Hearsons Cove and King Bay, with Sites 11, 12 and 13, and sites 14, 15, 16 and 17, respectively, were the most habitat-diverse areas with two small-scale habitats in Hearsons Cove (high-tidal alluvial fan and low-tidal shoals), and three small-scale habitats (tidal-creek shoals, ebb-tidal delta shoals, mid- to low-tidal shoals) in King Bay. Several of the sites studied along the study transects had soldier crabs occurring on two to three different habitat units within the local area (*viz.*, Coconut Well, Hearsons Cove, the Gascoyne Delta, and the Six-mile Creek area). While not part of the detailed study sites, similar to Hearsons Cove and King Bay, the Willie Creek area, north of Broome, illustrates habitat diversity, with soldier crab habitats developed on shoals of an ebb tidal delta, on sand flats and shoals within a tidal lagoon, and within a shoal complex on the open coast.

However, a relatively uniform, small-scale geomorphic unit functioning as a habitat does not necessarily mean that the distribution of soldier crabs is always continuous across the entire unit. In certain locations, and at different times, the crabs may be restricted to a specific section of the unit, as for example, shoal margins, or to a particular level of the tidal-creek bank, or even to micro-topographic features on a tidal flat (such as mounds, or hummocks, or sand ripples; see section on microtopography).

More detailed information and data for each of the soldier crab habitats located at the twenty-five study sites are presented in Tables 7 and 8 in terms of the abundance of the soldier crabs (as numerical and ranked data) during July 2004, together with key abiotic factors in the soldier crab habitat, *viz.*, gradient of shore, salinity of the open marine waters or tidal creek adjoining the soldier crab habitat, salinity of the tidal-flat groundwater, salinity of the pellicular water, sediment moisture content at low tide, sediment grain size, sediment composition (% of silicic grains, calcium carbonate grains, and organic carbon), % mud content, and % organic matter in the < 63 μm fraction, and (for Table 8) tidal level and frequency of flooding. These data can be used to characterise the soldier crab habitats sedimentologically, hydrologically, hydrochemically (salinity), and biochemically (organic matter).

Table 7 shows several patterns. For the replicate samples collected for many parameters, there is a relative consistency in value. For instance, at the smallest scale, the scale at which the soldier crab survives and goes about its diurnal tasks, there is a relative consistency during a low tide within a site and across the region of salinity of tidal-flat groundwater, salinity of pellicular water, and sediment moisture content. Aspects of the information and data in Table 7 are described below.

The abundance of soldier crabs across their biogeographic range for the different sites exhibited no regional pattern (Figure 9), *i.e.*, no increase or decrease in general abundance at the habitats sampled in relation to climate trends or tidal range trends.

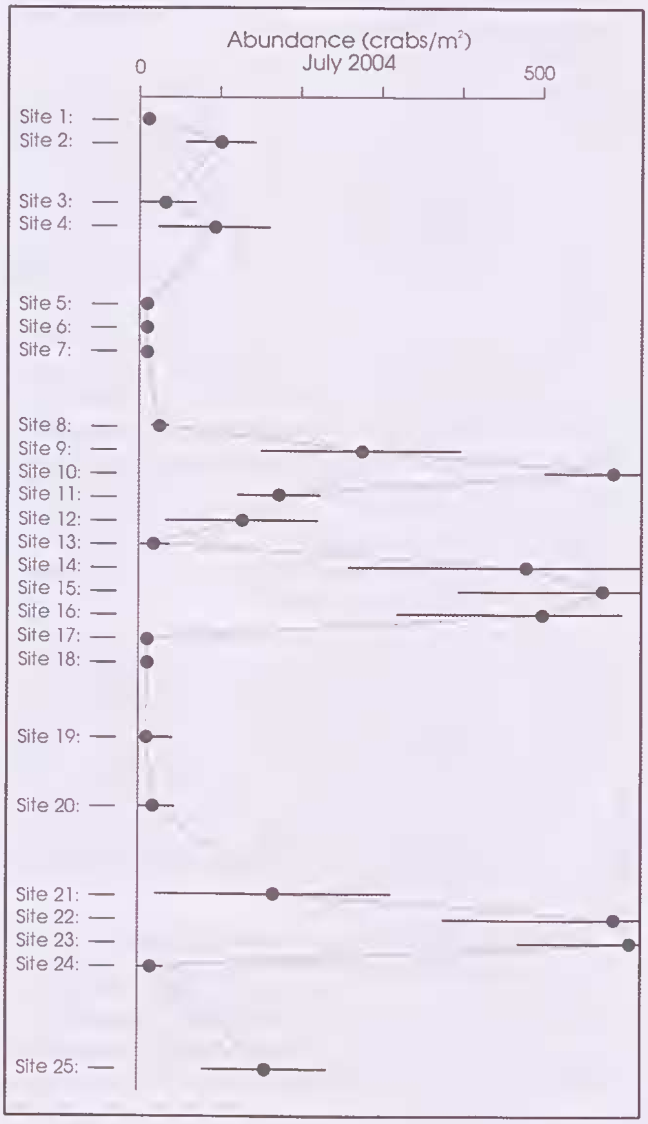


Figure 9. Abundance of soldier crabs in July 2004 at the various transects (arranged latitudinally).

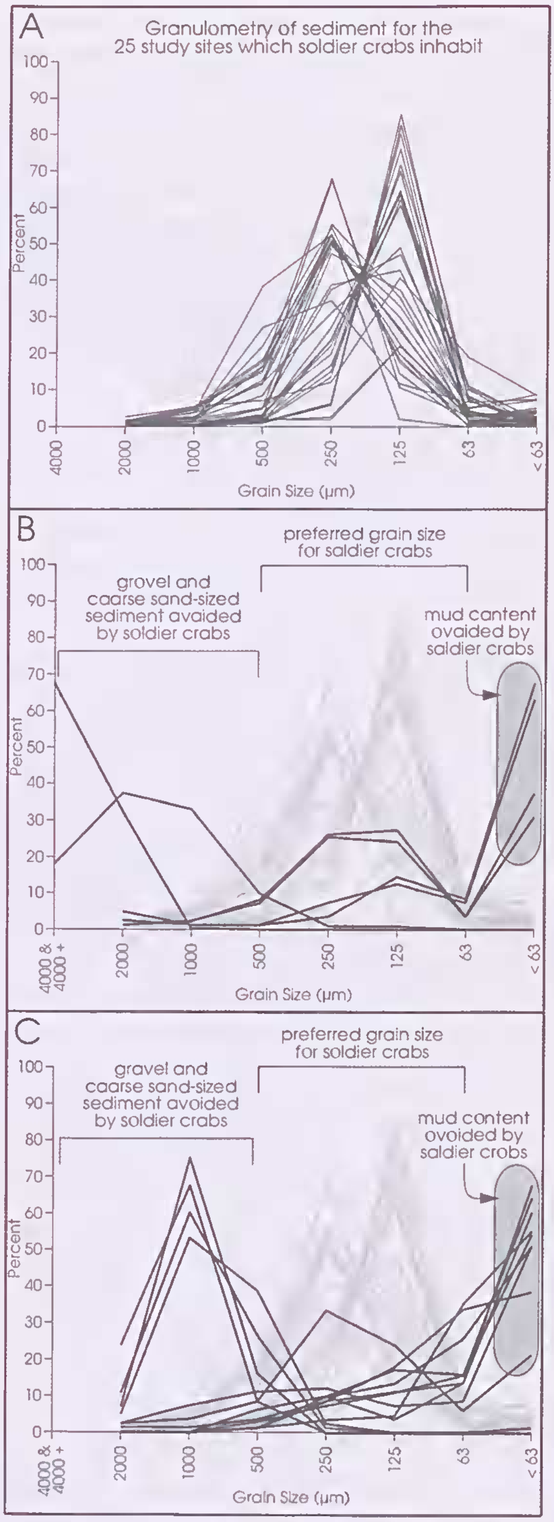


Figure 10. A. Granulometry of sand from all study sites that are soldier crab habitats [note that individual graphs of the grain-size distribution of a given sediment is unimodal – the apparent bimodal appearance of the combined presentation of all the graphs is due to the fact that half the graphs are modally centred on the 250 μm size and the other half centred on the 125 μm size]. B. Granulometry of the experimental blocks of sediment (black lines) which soldier crabs avoided in comparison to the granulometry of soldier crab habitat (grey lines). C. Granulometry of the coarser sediments and muddier sediments (black lines) that adjoin soldier crab habitats (and do not support the crabs) in comparison to the granulometry of soldier crab habitat (grey lines).

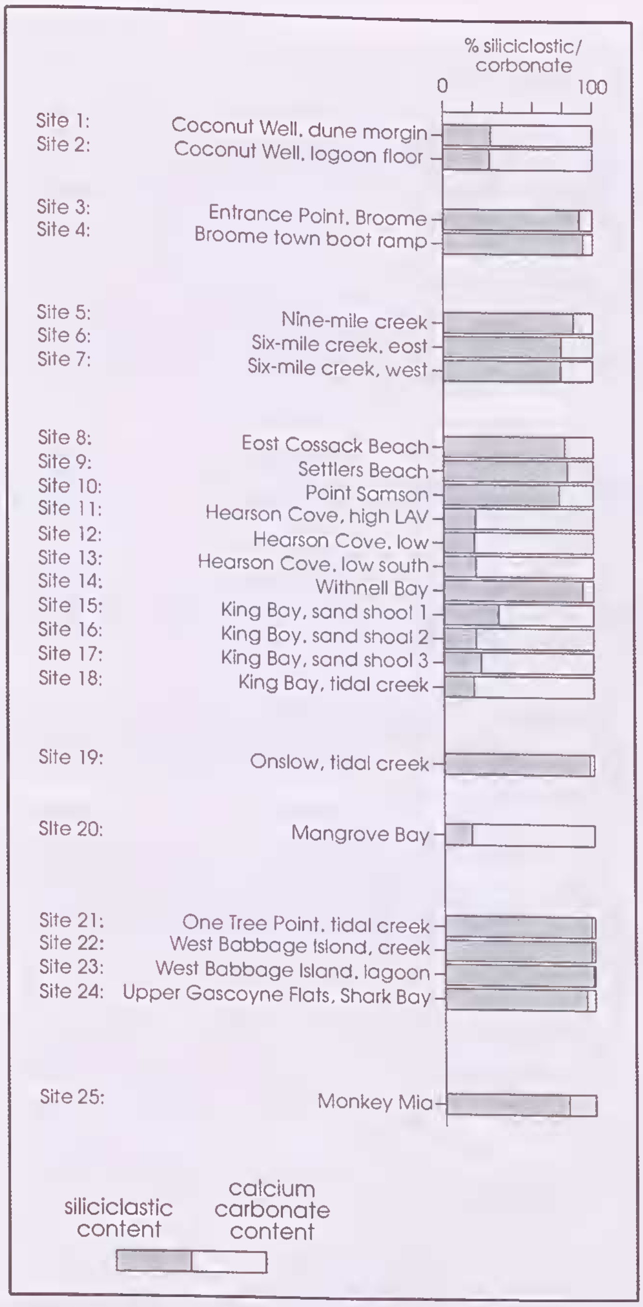


Figure 11. Composition of sand as siliciclastic or calcareous at the various transects (arranged latitudinally).

The open ocean waters and tidal-creek waters that deliver water to tidal flats to replenish their groundwater and pellicular water in the soldier crab habitat ranges from 31 to 38 ppt, the highest salinity being at Monkey Mia where salinity of open waters generally are elevated (Logan & Cebulski 1970). Open waters also are slightly elevated in salinity where tidal creeks have drained salt flats and delivered saline waters to the sea (*e.g.*, Sites 5, 6 and 7, at Port Hedland). Generally, the open waters tend to be normal oceanic salinity (~ 35 ppt) at most other sites. Groundwater salinity and pellicular water salinity in the soldier crab habitat are generally 31 to 45 ppt, and ~ 27 to 44 ppt respectively, depending on the level of the soldier crab habitat relative to MSL, and whether there is seepage maintaining the groundwater which may dilute its salinity to 27 ppt. Sediment moisture content at low tide generally is 16–39%.

The sediment samples from the twenty-five transects show the modal grain size of the soldier crab habitat, at most sites, to be a fine to medium sand (grain size 125–250 μm); at Site 7 it was medium to coarse sand (grain size 250–500 μm). Figure 10A shows the range of grain sizes from the various sites. Sands can vary from being dominated by silicic grains (mainly quartz) to those dominated by silicic grains or those dominated by calcium carbonate grains (Figure 11), and in general, regionally, there was no pattern to their composition except that deltas (such as the Gascoyne River Delta) tend to be dominated by silicic grains (sites 21–24). As such, sediment composition appears to make no difference to the occurrence of soldier crabs. Organic carbon content of the whole sediment tends to be low (< 1% varying to ~ 3%). The sediments with the highest carbon content are those that are proximal to or within mangrove formations (*e.g.*, Sites 11 and 12). Mud content, too, is generally low: usually < 1% varying up to 5%, but may be up to ~ 8%. Organic carbon content of the mud fraction (the fine-grained material that the crabs extract from the sand for feeding) is in the range of 3–22% depending on site. The sediment with the lowest content of organic carbon in the mud fraction corresponded with the lowest numbers of crabs.

Information on the local-scale features of the soldier crab habitat along a transect is provided in Figure 12, showing geomorphic units providing the soldier crab habitat, the topographic profile and surface gradients, the tidal level of the habitat, microtopography, sediment types, the extent of soldier crab zone along the profile and their relative population abundance (as ranked data), and some of the key processes. Typical views of selected sites are illustrated in the annotated photographs shown in Figure 13.

For comparative purposes between the twenty-five study sites, key abiotic parameters are graphed in Figure 14. The graphs show that for most abiotic parameters, even compared regionally, there is a narrow range of values in groundwater salinity, pellicular water salinity, % moisture of surface sediments, sediment grain size, mud content, and organic matter content in the soldier crab habitat.

While most of the information relating to habitat description and setting, and the description of the abiotic characteristics for each habitat at the various sites are presented in Tables 6, 7 and 8, key points from each of the transects are described below, with emphasis on factors that are especially of significance for that site (*e.g.*, tidal level of the habitat, or the salinity or moisture content where fresh water has resulted in dilution of hypersalinity). The reader should refer to Tables 6–8 to obtain details of setting, abiotic characteristics and salinity features of the site.

Site 1 shows *M. occidentalis* at the highest level of the tidal zone recorded in their biogeographic range, *i.e.*, ~ 1 m below HAT in an extreme macrotidal region of 10.5 m tides sheltered *within* a tidal lagoon. The crabs inhabit the sloping tidal margin of a dune where it makes contact with the tidal lagoon. Sustained by fresh-water seepage from the dune, the soldier crab habitat has a pellicular water content of ~ 20%, and a (diluted) groundwater and pellicular water salinity of ~ 42 ppt and 31 ppt, respectively, with seepage measured at 27

Table 6

Description of the twenty-five study sites including coastal setting, wave-energy, geomorphic unit, tidal level and extent of soldier crab habitat, surface gradient, and microtopography if applicable

Site 1 at Coconut Well borders the margin of a dune that forms the eastern margin of a barred tidal lagoon, sheltered from oceanic wave action by a sand barrier. The open coast is too high energy for soldier crabs. The soldier crab habitat is located ~ 1 m below HAT, and receives fresh-water seepage from the adjacent dunes; soldier crabs in medium abundance occupy a band *circa* 2 m wide and 20 m long amongst scattered, stunted mangroves (*Avicennia marina*, *Ceriops tagal* and *Aegialitis annulata*) and sea couch (*Sporobolus virginicus*).

Site 2 at Coconut Well is within the same barred tidal lagoon as Site 1. The lagoon is dominated by flood- and ebb-tidal currents that have formed low-relief sand shoals, and shallowly-incised tidal creeks. While occurring locally across the lagoon floor, soldier crabs tend to be dominantly along the margins of the shallowly-incised tidal creeks, generally occupying a narrow band approximately 1 m wide and 30 m long along the banks of the tidal creek; they also occur on the crest of sand shoals. The lagoon floor is moist enough and of low enough salinity in terms of groundwater and pellicular water for soldier crabs to inhabit because sand bars at the mouth of the barred lagoon retard tidal water and groundwater discharge.

Site 3 at Entrance Point is a wave-dominated, mid- to low-tidal beach fronting a rocky shore. Numerous stacks and outcrops of Mesozoic rock occur on the beach, providing local sites of relative shelter. Soldier crabs occur at approximately mid-tidal level, occurring in patches determined by local shelter of the rocky stacks and outcrops. The extent of the soldier crab zone is 10 m laterally and 2 m seaward.

Site 4 adjoining Broome town is a high-tidal, sandy spit-and-shoal area landward of the mangroves that front a cliff cut in semi-indurated red dune sand. The habitat is a relatively low-energy wave environment. Seawater seepage and fresh-water seepage maintain moisture levels in the sand, and maintain a relatively low groundwater and pellicular water salinity. Soldier crabs occur at approximately high spring tide level on the high-tidal flat in an area 20 m wide.

Site 5 at Nine-mile Creek is a sandy high-tidal flat adjoining a tidal creek in a limestone barrier coastal setting. The site is located well within the headwaters of a tidal creek, and behind and within mangrove shrubland, a setting which provides shelter from swell and wind waves; as such it is a relatively low-energy wave environment. Soldier crabs occur at approximately high neap tide level on the sandy tidal flat, occurring in patches in an area 20 m wide and extending 50 m seaward.

Site 6 at Six-mile Creek East is the base of the beach slope, at the interface between a moderately sloping beach surface and a low-gradient tidal flat, the latter sparsely populated with mangrove trees and shrubs and underlain by sand, muddy sand, mud, and limestone (pavement). The site is regionally protected from swell and wind waves by a Pleistocene limestone ridge to the north at the edge of the tidal flat. Soldier crabs occur mainly at the base of the beach slope and partly into the adjoining low-tidal sand flat, either on bare sand or sparsely among *Avicennia* pneumatophores. Seepage from the beach face, discharging along the shallow buried limestone pavement, maintains the moisture and salinity of the soldier crab habitat. At the base of the beach slope the soldier crab zone is 4 m long by 2 m wide.

Site 7 at Six-mile Creek West is a sandy tidal flat composed of sand flats and low sand shoals. As with Site 6, the location is regionally protected from swell and wind waves by a Pleistocene limestone ridge, and as such, the wave-energy is low to moderate. Soldier crabs occur mainly along the edge of a shore-normal, broad, linear, low-relief sand shoal at the mid-high tidal level. The soldier crab zone extends 20 m along the shoal edge and is 1 m wide.

Site 8 at Cossack East is a laterally-extensive beach shore developed along the margin of Butchers Inlet. Wave-energy is relatively low as the site is sheltered by a rocky headland to the north, and by its location in the interior of a large tidal creek. Soldier crabs occur on the mid-tidal sand slope adjoining the creek bank.

Site 9 at Settlers Beach is a laterally-extensive beach shore developed seaward of an emerged spit and dune along a ria coast. The site is regionally protected from swell and wind waves by peninsulas of rock. The shore is a moderately-sloping beach face, bordered by a low tidal flat composed of low-relief sand shoals (a shoal complex). Soldier crabs occur at two locations: (1) in a zone along the lower slope of the beach face, extending to the base of the slope (20 m lateral extent and 5 m wide seaward); and (2) on the series of shoals extending laterally along the beach for 200 m and seaward for 80 m.

Site 10 at Point Samson is another extensive beach shore developed seaward of an emerged spit and dune along a ria coast. The site is regionally protected from swell and wind waves by peninsulas of rock and Pleistocene limestone. The shore is a moderately sloping beach face, bordered by a low tidal flat composed of low-relief sand shoals (a shoal complex). The low-relief, shore-parallel, mid-tidal sand shoals form the soldier crab habitat. Soldier crabs occur in a 20 m x 20 m area within the shoals.

Site 11, at Hearsons Cove, is a high-tidal alluvial fan underlain by sand and gravelly sand. It is located landward of mangrove heath and open heath within a broad embayment in a ria coast. Occurring in the most sheltered part of Hearsons Cove, the site is regionally protected from swell and wind waves both by its location in the northern part of the Cove, and by the shelter afforded by the mangroves. There is fresh-water seepage from the alluvial fan, which has maintained moisture levels and salinity levels sufficient to support soldier crabs. Soldier crabs occur in a 10 m x 10 m area amongst the mangrove shrubland, but also in a fringe along the landward edge of the mangrove.

Site 12, at Hearsons Cove, is a mid-tidal sand shoal occurring seaward of mangroves. It is in a low wave-energy environment at the northern sheltered part of the Cove adjoining where mud begins to accumulate. Soldier crabs occur on mid-tidal, low-relief, shore-parallel sand shoals seaward of the mud deposits. The soldier crab zone extends 20 m seaward and is 5–10 m wide.

Table 6 (cont.)

Site 13, at Hearsons Cove, is located on a shoal complex that comprises a wave-energy-dissipative, low-gradient shore that adjoins a moderately-sloping, reflective beach. Located in the relatively sheltered central-northern part of the Cove, as with the other sites in Hearsons Cove, this site is a low wave-energy environment. At the base of the adjoining beach slope, there is seawater seepage which, through lateral seepage and ponding by the shoals, maintains moisture levels and salinity levels for the soldier crab habitat. Soldier crabs preferentially inhabit the margins of the shoals, forming zones tens of metres long and ~2 m wide, but also inhabit the crest of the shoal in lower density. Microtopographic features on the shoal include mounds (or hummocks) and depressions (with relative relief of 20 cm, respectively).
Site 14 at Withnell Bay, an embayment sheltered from swell and wind waves by its length, its narrow entrance, and its shelving (wave-energy-dissipative) sedimentary floor along the length of the embayment. The soldier crab habitat is located deep into the head of the embayment on a sand flat at the base of a slope cut into the seaward edge of mangroves. Seepage of seawater from the base of this slope maintains moisture levels and salinity levels for the soldier crab habitat. The soldier crab habitat is extensive, covering approximately a thousand square metres.
Sites 15 and 16 at King Bay are in a broad embayment within a ria coast in a low wave-energy setting. The habitats are regionally sheltered from swell and wind waves by their location deep within King Bay, and by the low-gradient, wave-energy-dissipative seafloor sloping from subtidal to intertidal. For these two sites, at the local scale, the habitats are locally protected by (ebb-tidal delta) shoals of 0.5–1.0 m relative relief (developed at the mouth of a tidal creek) that support copses of mangroves; the sites are leeward of mangrove-vegetated parts of the shoals; mid- to low-tidal sand flats surround the shoals. Soldier crabs occur on the margins of the shoals, and to a limited extent, on the adjacent tidal flat to approximately levels of the high tide neap tide. The soldier crab zone is extensive, covering tens of thousands of square metres. Microtopographic features on the tidal flat include mounds (or hummocks) and depressions (with relative relief of 20 cm, respectively). Within the mound-and-depression microtopography, soldier crabs preferentially inhabit the margins of the low-relief hummocks and avoid the often water-filled depressions.
Sites 17, at King Bay, is in the same geomorphic and oceanographic setting as Sites 15 and 16. The soldier crab habitat is located on the top of a sand bar, parallel to the front of mangroves further into the embayment, and therefore of lower wave energy than Sites 15 and 16. The bar, some 50 cm high, 20–30 m wide, and ~ 75 m long, is emergent above the surrounding muddy sand tidal flat.
Sites 18 is a shoal complex near the mouth of a tidal creek within King Bay. The creek is in the same geomorphic and oceanographic setting as Sites 15 and 16, but more protected because of its location in the axis of the creek. Low-relief sand shoals, 5–10 m wide and 30–50 cm high, dominate the centre of the tidal creek; the soldier crab habitat is located on the top of the shoals.
Site 19 is along the bank of a tidal-creek near Onslow in a limestone barrier and beach/dune shore complex. The habitat is developed at ~ MSL alongside, behind and within mangroves that fringe the creek bank. While the open coast is wave-dominated, the axis of the creek affords protection, and the soldier crab habitat receives low wave-energy. The soldier crab zone located at ~ MSL is 4 m wide and extends laterally along the creek bank for 10 m.
Site 20 at Mangrove Bay, northern North West Cape, is a pocket beach that adjoins a fringe of shoreline mangroves. While the open coast is wave-dominated, the pocket beach is protected from swell and wind waves by the Ningaloo Reef, by a near-shore spit complex, and by a wide wave-energy-dissipative, low tidal flat. The beach shore is a narrow reflective beach, has a relatively high gradient, and sharply adjoins the wide, wave-energy-dissipative low tidal flat. Seepage of seawater from the beach face, discharging along a shallow, buried muddy-sand layer, maintains the moisture and salinity of the soldier crab habitat. The soldier crab habitat is developed at ~ MSL at the base of the beach slope, alongside and partly into mangroves that fringe the shore. The soldier crab zone is < 1 m wide, and extends laterally along the beach for 10 m.
Sites 21 and 22, at One Tree Point and East Babbage Island, are tidal creeks within the Gascoyne River Delta complex. The habitats are on the delta strand plain, fully sheltered from regional swell and wind waves by low-relief dune barriers and beach ridges. Wave energy is low and the soldier crabs inhabit the tidal-creek banks and a point bar shoal at the mid- to high-tide level. In the East Babbage Island location the soldier crabs are partly on bare sand and partly amongst pneumatophores associated with scattered, stunted mangrove shrubs. Both tidal-creek banks, being of moderate slope, have high internal drainage, and so the soldier crab zone is relatively narrow. The soldier crab zone has a lateral extent of 10 m and a width of 2 m at One Tree Point, and 5 m long and 0.5 m wide at East Babbage Island.
Site 23 at West Babbage Island is within a tidal lagoon within the Gascoyne River Delta strand plain. Being on the strand plain, the habitat is fully sheltered from regional swell and wind waves by low-relief dune barriers and beach ridges, and hence wave energy is low. The soldier crabs inhabit the mid-tidal to low-tidal level of the lagoon. The soldier crab zone has a lateral extent of 10 m and a width of 2 m. Surface gradient is low.
Site 24 at Gascoyne Flats, is the tidally-exposed part of a spit and mangrove shore that forms the edge of the Gascoyne Flats (a seagrass complex that is the north-eastern part of the Wooramel Seagrass Bank of Shark Bay). The habitat is sheltered from regional swell by the limestone barriers of Edel Land and Dorre Island, and semi-protected from wind waves by the buffering and dampening effect of the seagrass meadows seaward of the site, hence wave energy is relatively low. Soldier crab habitats are developed on small pocket (tidal) beaches whose surface gradient is low; these beaches occur between copses of mangroves. The extent of the soldier crab zone is a ribbon 20 m long and extending 5 m seaward. The sediment surface is smooth except for lines of seawrack.
Site 25 at Monkey Mia is on a spit shore of the metahaline middle part of a seagrass bank in Shark Bay. The habitat is fully sheltered from regional swell by the limestone barriers of Peron Peninsula, Edel Land and Dorre Island, and semi-protected from wind waves by the buffering and dampening effect of a large, seagrass-vegetated, submarine spit located seaward of the site, hence wave-energy is relatively low. Soldier crabs occur on a broad, low-relief, mid-tidal sand shoal landward of the spit. The habitat is 20 m wide and extends 27 m seaward. The shoal surface is rippled with low, broad sand ripples (1–2 cm high and 5–10 cm wide).

Table 7

Population abundance and details of abiotic environmental parameters for the soldier crab habitats at the twenty-five regional study sites ($x \pm \sigma$; na = not applicable)

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8	Site 9	Site 10	Site 11	Site 12	Site 13
Abundance (no. crabs/m^2 $x \pm \sigma$, and ranked abundance)	10 ± 0.1 low	102 ± 58 medium	32 ± 41 low	93 ± 67 low	9 ± 1 low	10 ± 0.1 low	10 ± 0.3 low	27 ± 9 low	275 ± 126 medium	589 ± 87 high	176 ± 52 medium	134 ± 100 medium	18 ± 19 low
Slope gradient	1:5 high	1:100 low	1:50 low	1:40 low	1:130 low	1:120 low	1:250 low	1:25 low	1:70 medium	1:100 low	1:50 low	1:50 low	1:500 low
Ocean or tidal creek salinity (ppt); creek salinity in [ ]	35.6 ± 0.2 [33.8 ± 0.1]	35.6 ± 0.2 [33.8 ± 0.1]	35.6 ± 01	35.6 ± 0.2	[36.7 ± 0.2]	36.9 ± 0.1 *	36.9 ± 0.1 *	35.6 ± 0.2	34.6 ± 0.2	33.9 ± 0.2	35.8 ± 0.1 *	35.8 ± 0.1 *	35.8 ± 0.1 *
seepage salinity (ppt)	27.1 ± 0.3	na	33.5 ± 0.2	31.1 ± 0.1	na	37.3 ± 0.4	na	na	na	na	na	na	na
Groundwater salinity (ppt)	42.2 ± 0.2	39.9 ± 4.3	35.0 ± 0.1	39.5 ± 0.3	44.5 ± 0.2	38.5 ± 0.1	38.6 ± 0.1	42.1 ± 0.5	39.0 ± 1.4	34.7 ± 0.1	43.9 ± 0.1	38.9 ± 0.4	37.0 ± 0.3
Pellicular water salinity (ppt)	31.0 ± 3.7	42.3 ± 1.4	41.7 ± 0.4	37.8 ± 1.0	43.0 ± 2.1	37.2 ± 1.2	44.2 ± 1.0	38.5 ± 0.5	37.1 ± 6.1	34.1 ± 3.3	41.8 ± 4.0	31.8 ± 3.1	33.2 ± 1.4
Sediment moisture (%)	20.1 ± 0.4	19.5 ± 3.5	18.2 ± 2.1	16.0 ± 0.3	21.7 ± 0.6	15.7 ± 4.7	21.2 ± 0.9	23.2 ± 0.5	20.0 ± 0.5	23.5 ± 1.9	38.9 ± 4.6	27.1 ± 2.0	31.9 ± 2.5
Sediment modal grain size (μm)	125 μm	125 μm	125 μm	125 μm	125 μm	125 μm	500 μm 250 μm	125 μm	125 μm	125 μm	125 μm	250 μm	250 μm
Sediment siliciclastic content (%)	29.5 ± 0.3	29.4 ± 0.4	90.8 ± 2.2	93.1 ± 0.5	85.4 ± 0.2	77.6 ± 6.4	77.3 ± 4.0	79.5 ± 0.5	81.5 ± 1.2	75.1 ± 1.0	17.6 ± 1.6	17.6 ± 2.5	18.1 ± 0.7
Sediment calcium carbonate content (%)	68.0 ± 0.3	68.8 ± 0.6	8.6 ± 2.1	6.4 ± 0.5	13.0 ± 0.5	21.1 ± 6.1	21.3 ± 4.4	19.0 ± 0.8	17.1 ± 1.2	22.7 ± 1.0	79.0 ± 1.7	79.7 ± 2.5	78.7 ± 0.9
Sediment organic carbon content (%)	2.45 ± 0.2	1.8 ± 0.2	0.6 ± 0.1	0.5 ± 0.0	1.6 ± 0.1	1.2 ± 0.4	1.4 ± 0.4	1.5 ± 0.1	1.4 ± 0.1	2.1 ± 0.2	3.4 ± 0.2	2.7 ± 0.2	3.2 ± 0.2
Sediment mud content (%)	0.1 ± 0.0	2.23 ± 0.2	0.82 ± 0.1	0.7 ± 0.0	0.1 ± 0.0	0.2 ± 0.0	0.5 ± 0.0	1.8 ± 0.1	1.31 ± 0.1	1.69 ± 0.2	8.4 ± 0.2	7.4 ± 0.2	5.1 ± 3.6
Organic matter in mud (%)	16.7 ± 0.5	6.4 ± 0.7	15.7 ± 0.4	15.6 ± 0.7	10.0 ± 1.1	3.4 ± 0.2	2.8 ± 0.3	18.7 ± 0.5	11.6 ± 0.1	14.7 ± 0.5	6.2 ± 1.3	3.3 ± 0.2	15.8 ± 0.4
Sediment type	carbonate	carbonate	silicic	silicic	silicic	silicic	silicic	silicic	silicic	silicic	carbonate	carbonate	carbonate

Table 7 (cont.)

	Site 14	Site 15	Site 16	Site 17	Site 18	Site 19	Site 20	Site 21	Site 22	Site 23	Site 24	Site 25
Abundance (no. crabs/m^2 x ± σ, and ranked abundance)	474 ± 214 high	573 ± 181 high	499 ± 190 high	10 ± 0.3 low	10 ± 0.3 low	11 ± 16 low	16 ± 0.1 low	171 ± 156 medium	589 ± 210 high	614 ± 143 high	19 ± 20 low	157 ± 73 medium
Slope gradient	1:50 low	1:500 low	1:50 low	1:400 low	1:75 low	1:10 medium	1:3 high	1:20 medium	1:20 medium	1:150 low	1:80 low	1:80 low
Ocean or tidal creek salinity (ppt); creek salinity in [ ]	38.7 ± 0.1	34.5 ± 0.1	34.5 ± 0.1	34.5 ± 0.1	[31.3 ± 0.3]	[32.0 ± 0.4]	37.0 ± 0.2	[35.9 ± 0.1]	[35.3 ± 0.4]	[35.3 ± 0.2]	33.5 ± 0.3	38.3 ± 0.3
Seepage salinity (ppt)	na	na	na	na	na	na	na	na	na	na	na	na
Groundwater salinity (ppt)	45.5 ± 0.7	38.7 ± 0.1	38.7 ± 0.1	37.0 ± 14	31.3 ± 0.3	32.0 ± 0.9	33.8 ± 0.5	37.3 ± 0.4	36.9 ± 0.3	35.7 ± 0.1	34.3 ± 0.4	37.1 ± 0.8
Pellicular water salinity (ppt)	34.6 ± 0.5	38.8 ± 2.2	38.9 ± 2.7	36.2 ± 3.7	29.6 ± 0.4	35.4 ± 2.6	35.6 ± 3.4	37.3 ± 2.2	31.5 ± 1.7	33.4 ± 1.1	26.7 ± 0.9	42.5 ± 1.3
Sediment moisture (%)	24.0 ± 0.7	28.6 ± 0.6	28.8 ± 2.3	26.9 ± 1.8	26.0 ± 0.2	16.8 ± 0.7	21.2 ± 1.8	19.9 ± 2.0	18.1 ± 0.7	18.8 ± 1.6	19.5 ± 1.1	17.2 ± 1.3
Sediment modal grain size (μm)	125 μm	125 μm	125 μm	250 μm	250 μm	125 μm	250 μm	250 μm	250 μm	250 μm	250 μm	250 μm
Sediment siliciclastic content (%)	91.0 ± 2.0	33.2 ± 1.2	19.6 ± 0.3	21.9 ± 1.6	16.5 ± 0.5	95.3 ± 0.2	15.6 ± 4.9	97.2 ± 0.4	97.3 ± 0.4	98.2 ± 0.2	94.1 ± 1.9	81.8 ± 8.2
Sediment calcium carbonate content (%)	7.1 ± 1.8	63.6 ± 1.1	78.6 ± 0.4	75.2 ± 1.3	80.2 ± 0.6	2.9 ± 0.2	82.0 ± 4.3	2.2 ± 0.4	2.2 ± 0.3	1.0 ± 0.1	5.5 ± 1.9	17.6 ± 8.0
Sediment organic carbon content (%)	1.9 ± 0.2	3.2 ± 0.1	1.8 ± 0.2	2.9 ± 0.3	3.3 ± 0.2	1.8 ± 0.1	2.4 ± 0.6	0.6 ± 0.1	0.4 ± 0.1	0.8 ± 0.2	0.5 ± 0.1	0.7 ± 0.2
Sediment mud content (%)	1.7 ± 0.3	2.8 ± 0.3	2.9 ± 0.2	4.1 ± 0.8	3.4 ± 0.7	1.2 ± 0.2	4.2 ± 0.5	2.9 ± 0.2	1.4 ± 0.1	2.2 ± 0.3	0.5 ± 0.0	0.9 ± 0.1
Organic matter in mud (%)	18.0 ± 0.4	12.6 ± 0.2	16.2 ± 0.3	18.7 ± 0.6	22.4 ± 0.1	10.4 ± 0.1	9.4 ± 6.6	12.9 ± 0.2	12.9 ± 0.9	13.7 ± 0.3	23.4 ± 0.2	16.2 ± 0.1
Sediment type	silicic	carbonate	carbonate	carbonate	carbonate	silicic	carbonate	silicic	silicic	silicic	silicic	silicic

* Sites 6 and 7 have the same open ocean water source; sites 11, 12 and 13 have the same open ocean water source; sites 15, 16 and 17 have the same open ocean water source

Table 8

Tidal level and frequency of flooding for the soldier crab habitats at the twenty-five regional study sites

Site	Tidal range setting (LAT-HAT) (m)	Tidal level or interval that the habitat occupies	Frequency of flooding (%)
1	10.5	~ 1 m below HAT	3.8
2	10.5	MHWS to 15 cm below MHWS	4 – 5.5
3	10.5	50 cm above and 60 cm below MHWN	27 – 43
4	10.5	20 cm above and 80 cm below MHWS	5 – 10
5	7.5	50 cm above and 70 cm below MHWN	36 – 51
6	7.5	between MSL and MHWN, 35 cm above MSL	42
7	7.5	located between MSL and MHWN, 25 cm above MSL	45
8	6.2	located between MHWN and 25 cm below MHWN	33 – 40
9	6.2	MLWN to MSL	51 – 65
10	6.2	MLWN to 50 cm below MSL	64 – 65
11	5.1	115 cm above MSL (a level between MHWN and MHWS)	14
12	5.1	MSL to 25 cm below MSL	51 – 58
13	5.1	MSL to 25 cm below MSL	51 – 58
14	5.1	20 cm above MLWN to MSL	51 – 62
15	5.1	MLWN to MSL	51 – 65
16	5.1	MLWN to MSL	51 – 65
17	5.1	MLWN to MSL	51 – 65
18	5.1	25 cm below MSL to MLWN	58 – 65
19	3.0	MSL to MLWN	47 – 64
20	2.8	MSL	50
21	2.0	MLWN to MSL	52 – 58
22	2.0	MHWN to MSL	36 – 52
23	2.0	MHWN to MSL	36 – 52
24	2.0	MLWN to MSL	52 – 67
25	1.5	MLWN	67

ppt. The site illustrates the extreme tidal levels that soldier crabs can occupy if grain size, moisture levels and salinity are correct for habitat development.

Site 2 shows soldier crabs at MHWS on the sandy floor of the same protected tidal lagoon described above. At MHWS, a level that is normally drier and more saline than the lower tidal levels, the lagoon floor is moist enough, and of low enough salinity, even during neap tides, for soldier crabs to inhabit because a sand bar retards tidal and groundwater discharge. The site again illustrates the extreme tidal levels that soldier crabs can occupy if grain size, moisture levels, and salinity are correct for habitat development.

Site 3 is a wave-agitated, moderately-sloping beach, and soldier crabs (though in low abundance) inhabit very localised sheltered areas at tidal levels of ~ MLWN, developed by small outcrops of Mesozoic rock. The site illustrates that very restricted shelter on high-energy beaches can provide localised soldier crab habitat.

Site 4 shows *M. occidentalis* at the level of MHWS, sheltered on a high-tidal sand flat in an extreme macrotidal region, landward of wide mangrove formation. While at MHWS, seawater/fresh-water seepage from the sandy beach and the sandy hinterland develops a moisture content and a diluted groundwater and pellicular water to support soldier crabs. The site illustrates the extreme tidal levels that soldier crabs can inhabit if protected by mangroves, and if grain size, moisture levels, and salinity are correct for habitat development.

Site 5 is a soldier crab habitat within a sandy area *within* mangrove shrubland flanking a tidal creek at ~ MHWN. The sand surface is wet enough for soldier crabs, and has a groundwater and pellicular water of ~ 44 ppt and 43 ppt, respectively. The site illustrates that soldier crabs can inhabit sandy mangrove-vegetated areas.

Site 6 is a soldier crab habitat between MSL and MHWN, at the base of a moderately-sloping, mid-tidal beach. Ebb-tide seepage of seawater from the beach sand (along a stratigraphic interface) dilutes groundwater and pellicular water, and keeps the sandy surface wet. The site illustrates that seepage from a beach face can develop a localised soldier crab habitat.

Site 7 is a soldier crab habitat on an open, sandy, low-tidal flat area located between MSL and MWN, bordering a shore-normal, low-relief sandy shoal.

Site 8 is a soldier crab habitat on an open, sandy, mid-tidal flat at ~ MHWN. Ebb-tide seepage of seawater dilutes the normally hypersaline groundwater and pellicular water and keeps the sandy surface moist.

Sites 9 and 10 are similar in that soldier crabs inhabit an open low-tidal sand flat between MLWN and ~ MSL, commencing at the base of a beach slope. The habitats are partially sheltered by shoals and depressions, and the sites illustrate local shelter can be developed within a shoal complex, with soldier crabs occurring on dissipative shores seaward of a reflective beach.

Site 11, between MHWN and MHWS, is at the landward edge of mangrove vegetation on a high-tidal alluvial fan of sand and gravelly sand. Seepage of fresh water from the hinterland into the alluvial fan dilutes the normally hypersaline groundwater and pellicular water and keeps the sandy surface moist. In this location the soldier crabs also partially inhabit sandy substrates amongst the mangrove pneumatophores where mangroves inhabit the edge of the alluvial fan. The site illustrates that seepage from an alluvial fan can develop a local soldier crab habitat, and that they can occur amongst mangrove pneumatophores.

Site 12, between MSL and MLWN at Hearsons Cove, is seaward of mangrove low forest, and is regionally well sheltered from swell and wind waves (see Hearsons Cove in Case Studies). This site illustrates the extent that shelter plays in the development of soldier crab habitats.

Site 13, between MSL and MLWN at Hearsons Cove, is on the margins of shore-parallel shoals in a shoal complex on the low tidal flats. Seepage of seawater from the beach face is ponded by the shoal. The ponded water maintains the moisture and salinity as a soldier crab habitat along the margins of the shoals. The site also is regionally sheltered from swell and wind waves (see Hearsons Cove in Case Studies). The site illustrates that local shelter can be developed within a shoal complex, and the extent that local hydrology plays in developing their habitat.

Site 14, located between ~ MSL and MLWN deep within a linear embayment, is seaward of mangrove low forest.

Sites 15 and 16, between MSL and MLWN on a sandy tidal flat, are located leeward of low-relief mangrove-vegetated shoals as part of an ebb-tidal delta. The sites illustrate the extent that local shelter can play in developing soldier crab habitats, as the soldier crabs occur dominantly leeward of the mangrove-vegetated shoals.

Site 17, a low-relief shore-parallel linear sand bar, between MSL and MLWN, is located deeper into King Bay than sites 14 and 15 where there is relatively more shelter from regional swell and wind waves. The sand bar, of 30 cm relative relief above the surrounding tidal flat, is surrounded by slightly more muddy sand wherein soldier crabs are absent. The site illustrates the extent that distance into any embayment (thus providing shelter from waves), and the emergence of a sandy bar surrounded by muddy sand play in the development of a soldier crab habitat.

Site 18 is a series of low-relief, mega-rippled sand waves and shoals, located between MLWN and ~ MSL, along the axis of a tidal creek within King Bay. It is the sandy site in King Bay that is most sheltered from regional swell and wind waves. The site illustrates that a sand-floored tidal-creek axis, protected from waves, can provide a soldier crab habitat.

Site 19, near Onslow, is a moderately-sloping, sandy bank of a tidal creek located between ~ MSL and MLWN, locally inhabited by mangroves. The soldier crab habitat receives seepage of fresh water and seawater from the upper creek bank. Being of moderate slope, the bank has high drainage and so the soldier crab zone is narrow. The site illustrates that a sand-floored tidal-creek bank, protected from waves, can provide a soldier crab habitat.

Site 20 shows a soldier crab habitat at ~ MSL at the base of a moderately-sloping, mid-tidal beach. Ebb-tide seepage of seawater from the beach dilutes groundwater and pellicular water and keeps the sandy surface wet. As with Site 6, this site illustrates that seawater seepage from a beach face can develop a localised soldier crab habitat.

Sites 21 and 22, at MLWN to MSL and MSL to MHWN, respectively, are the sandy point bar and bank of meandering tidal creeks on a strand plain of a delta. The point bar and bank, being of moderate slope, have high internal drainage, thus the soldier crab zone is narrow. The sites illustrate that a sand-floored tidal-creek point bar and bank, protected from waves, can provide a soldier crab habitat.

Site 23, at ~ MSL to MHWN, is a sandy low-tidal flat of a lagoon on a strand plain of a delta. The site illustrates that a sand-floored tidal lagoon, protected from waves, provides a soldier crab habitat. It is similar to Site 2 in setting, though at a lower tidal level.

Site 24, at ~ MSL to MLWN, is the sandy tidal flat that occurs landward of a wide seagrass bank. The site illustrates the development of soldier crab habitat leeward of the sub-regional wave-dampening effect of seagrass meadows offshore, and upslope of a dissipative shore.

Site 25 is at MLWN on a sandy low-tidal flat, locally protected by a small, shoreline, recurved spit, the entire complex occurring landward of seagrass banks (and a large submerged seagrass-vegetated spit) in the middle of Shark Bay. The site illustrates the development of a soldier crab habitat leeward of the sub-regional wave-dampening effect of seagrass meadows offshore, combined with the local shelter of a shoreline recurved spit.

The relationship of soldier crab habitat to geomorphic units and hydrologic zones, for the twenty-five transect sites, is summarised in Table 9.

Table 9

Relationship of soldier crab habitat to geomorphic units and hydrologic zones

Geomorphic unit	Transect site
emergent sandy bars and shoals on a dissipative shore	sites 7, 9, 10, 12, 13, 17
sandy bank and shoals of tidal creek	sites 2, 5, 18, 19, 21, 22
dissipative sandy shore	sites 18, 14, 24
sand-floored tidal lagoon	sites 2, 21, 23
sandy ebb-tidal delta shoals, protected by low headland	sites 15, 16
seawater seepage zone, base of a beach slope	sites 6, 20
freshwater seepage zone, high tidal sand	sites 1, 11
protected sandy zone landward of mangroves	sites 4, 11
sandy beach, with local protected zones behind spit	site 25
sandy beach, with local protected zones amongst rock outcrop	site 3

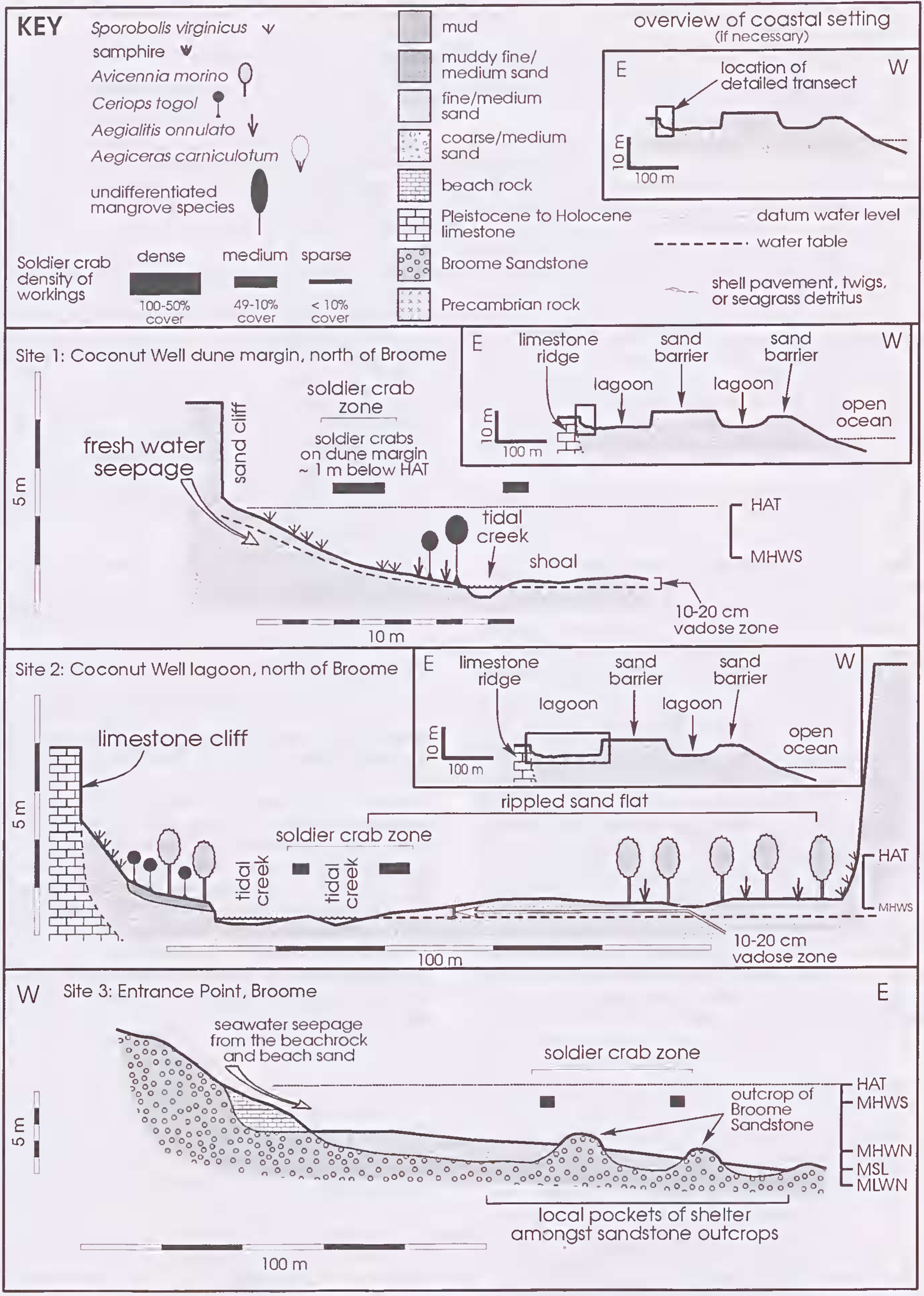


Figure 12. Transects through the twenty-five study sites in July 2004 showing profiles, sediment types as substrates, vegetation, groundwater table level at low tide, some geomorphic features specific to the transect, some hydrologic processes specific to a transect, and the occurrence of soldier crabs on the profile shown in ranked abundance.

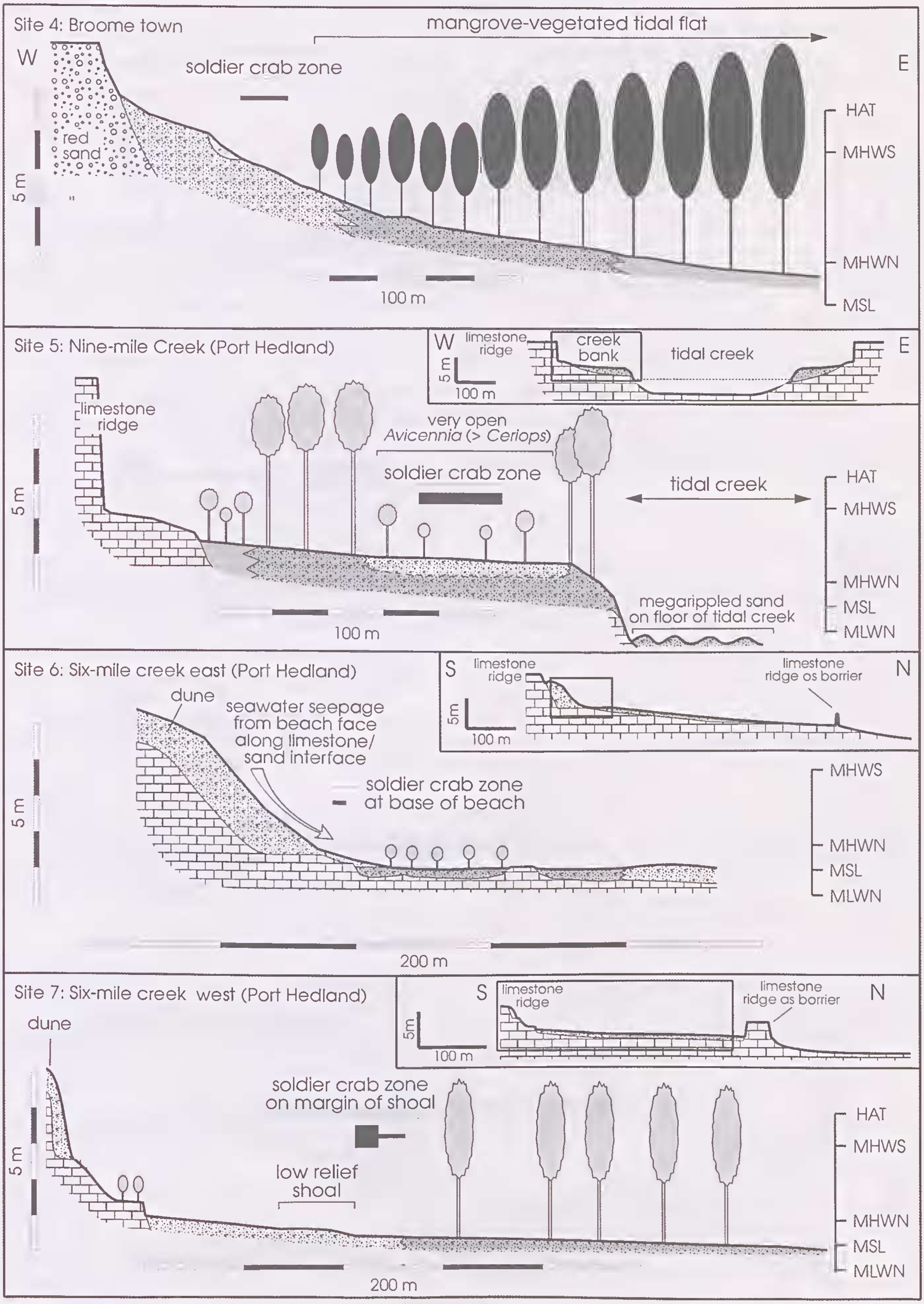
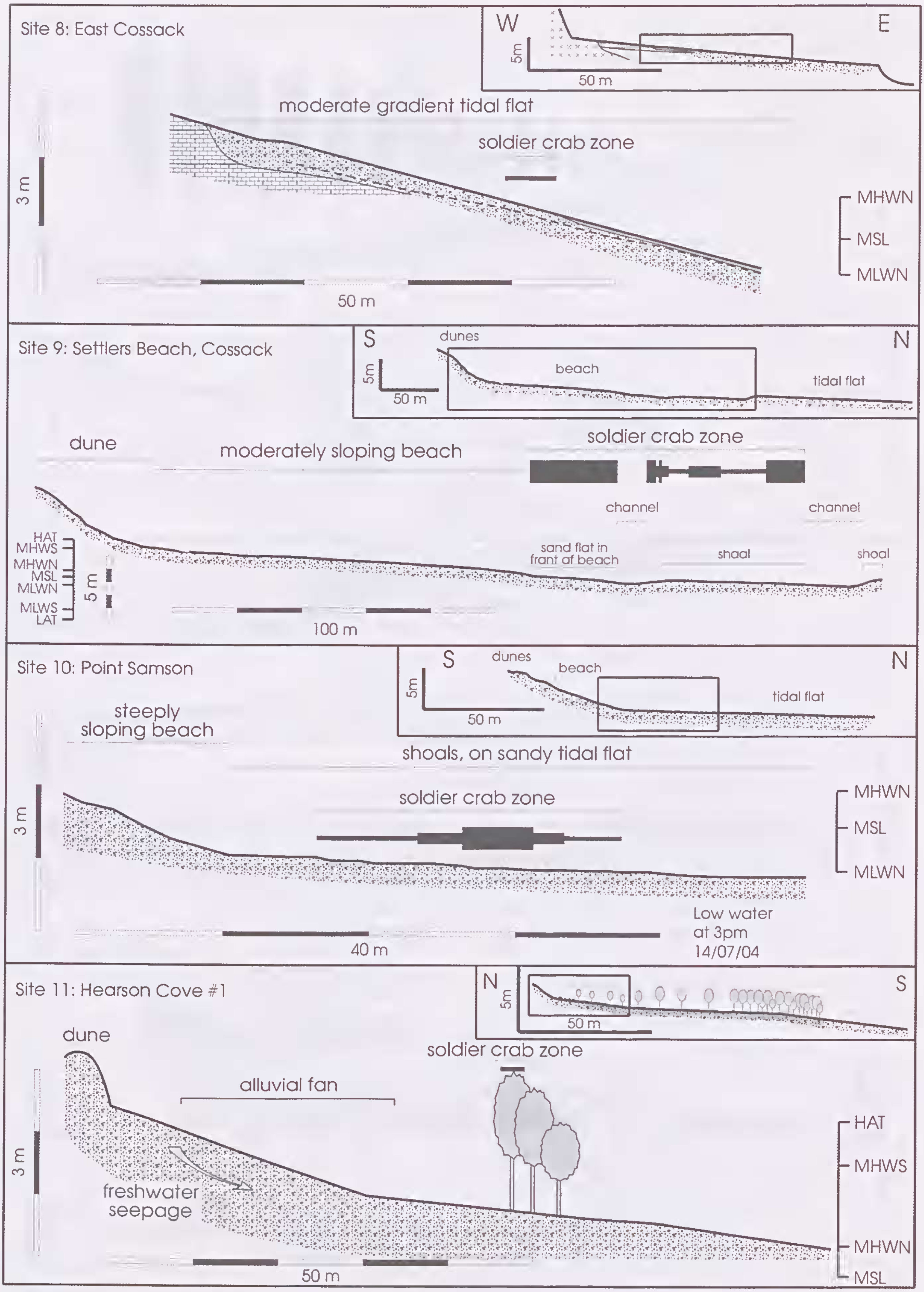


Figure 12 (cont.)



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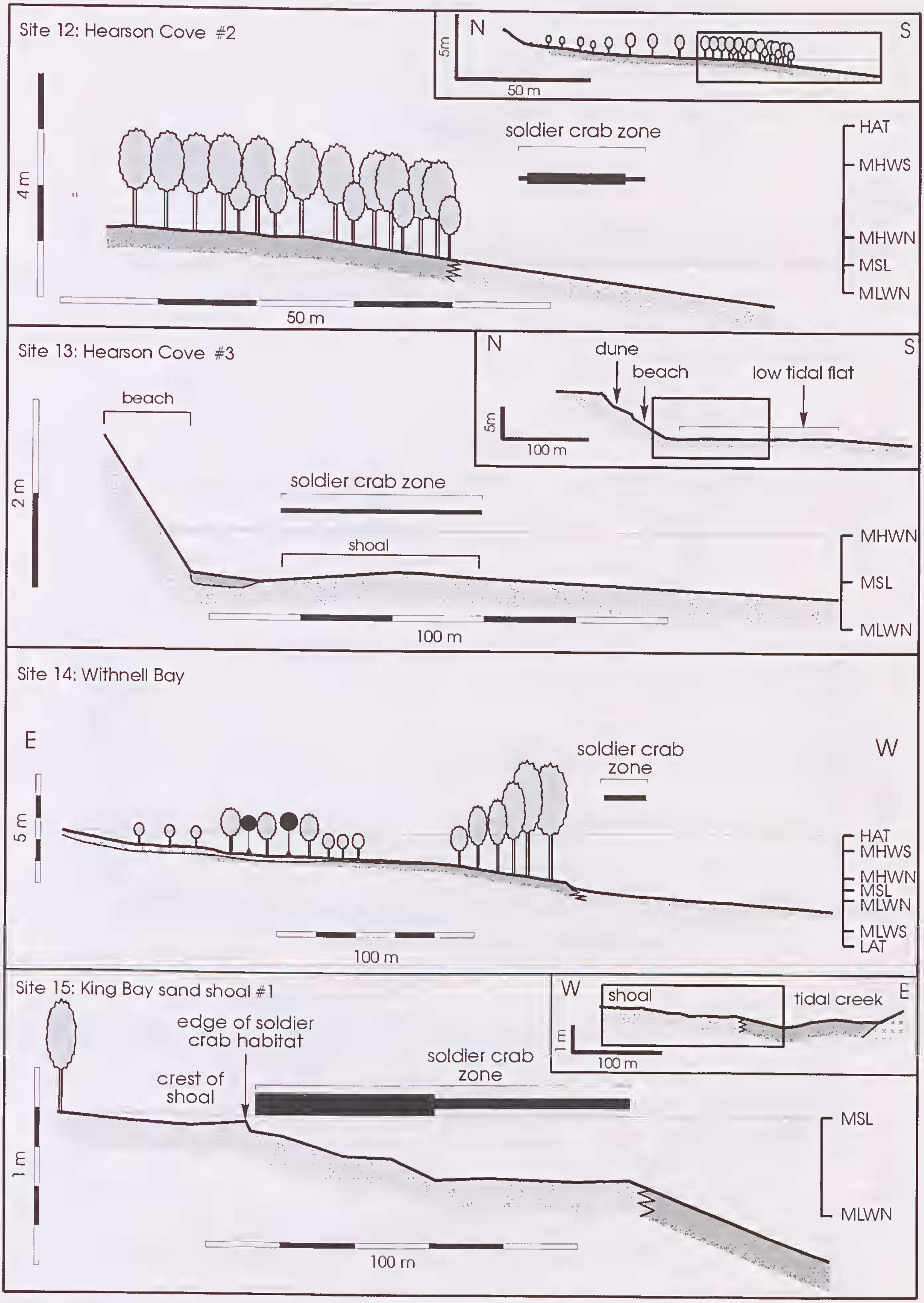

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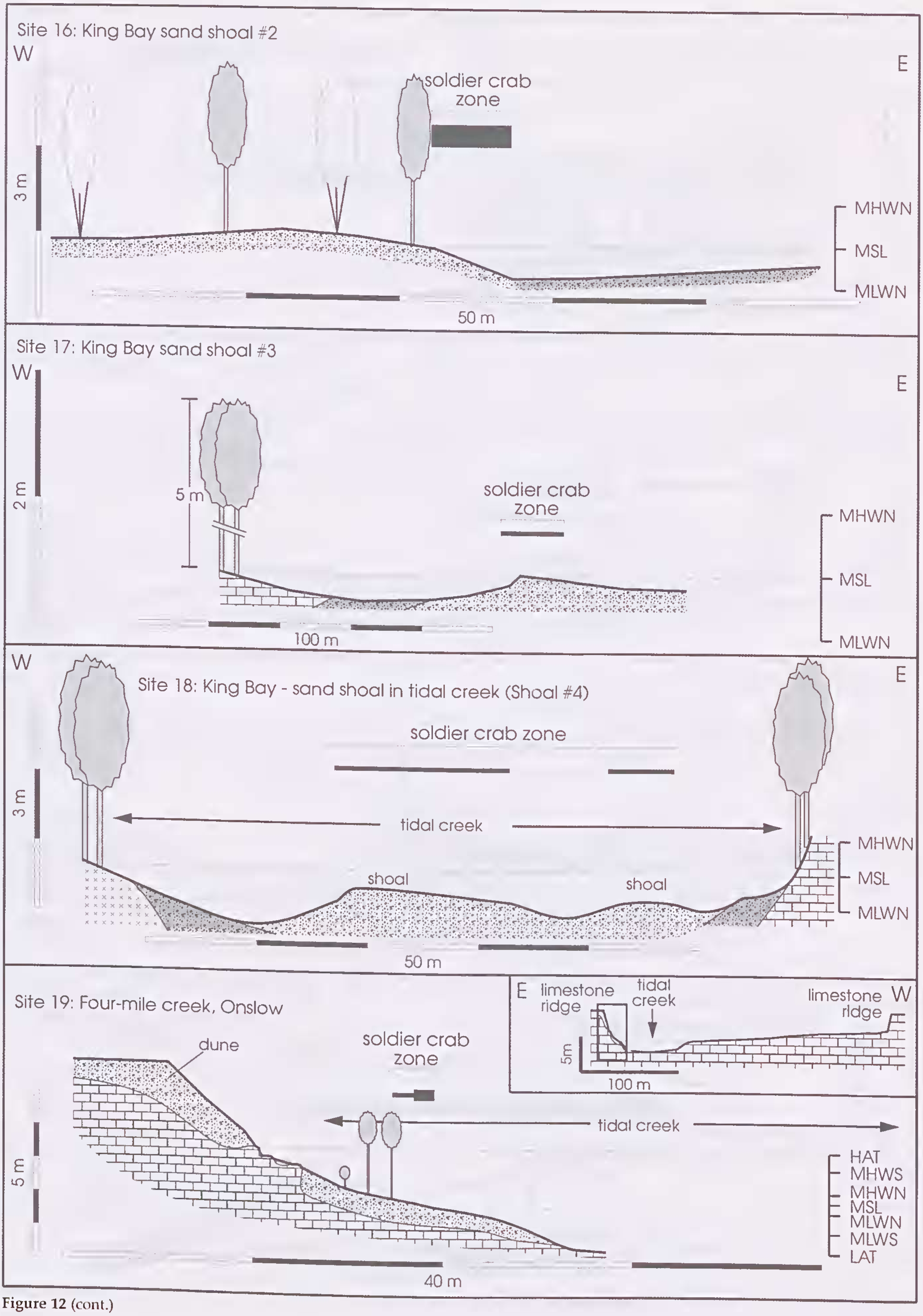

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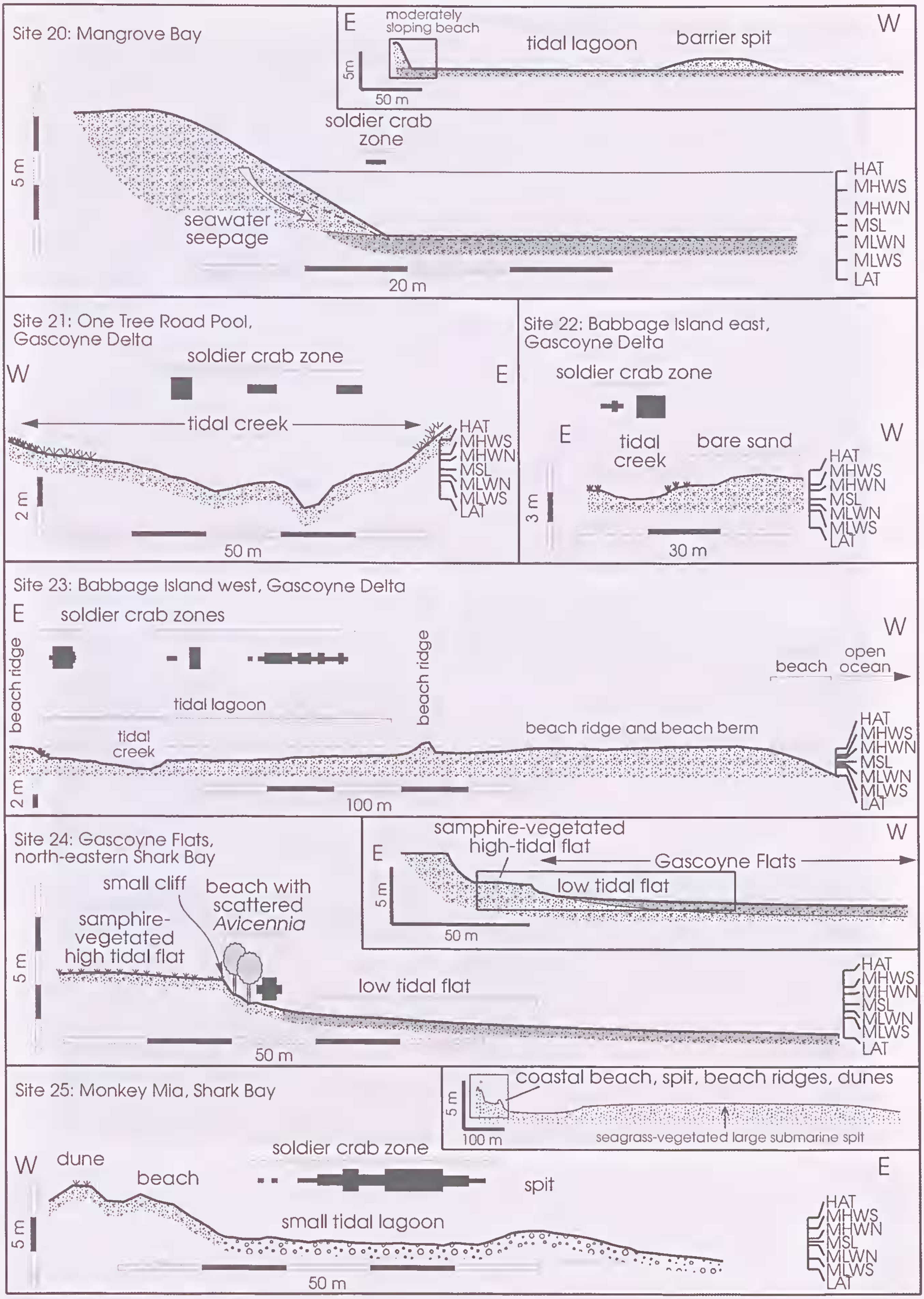

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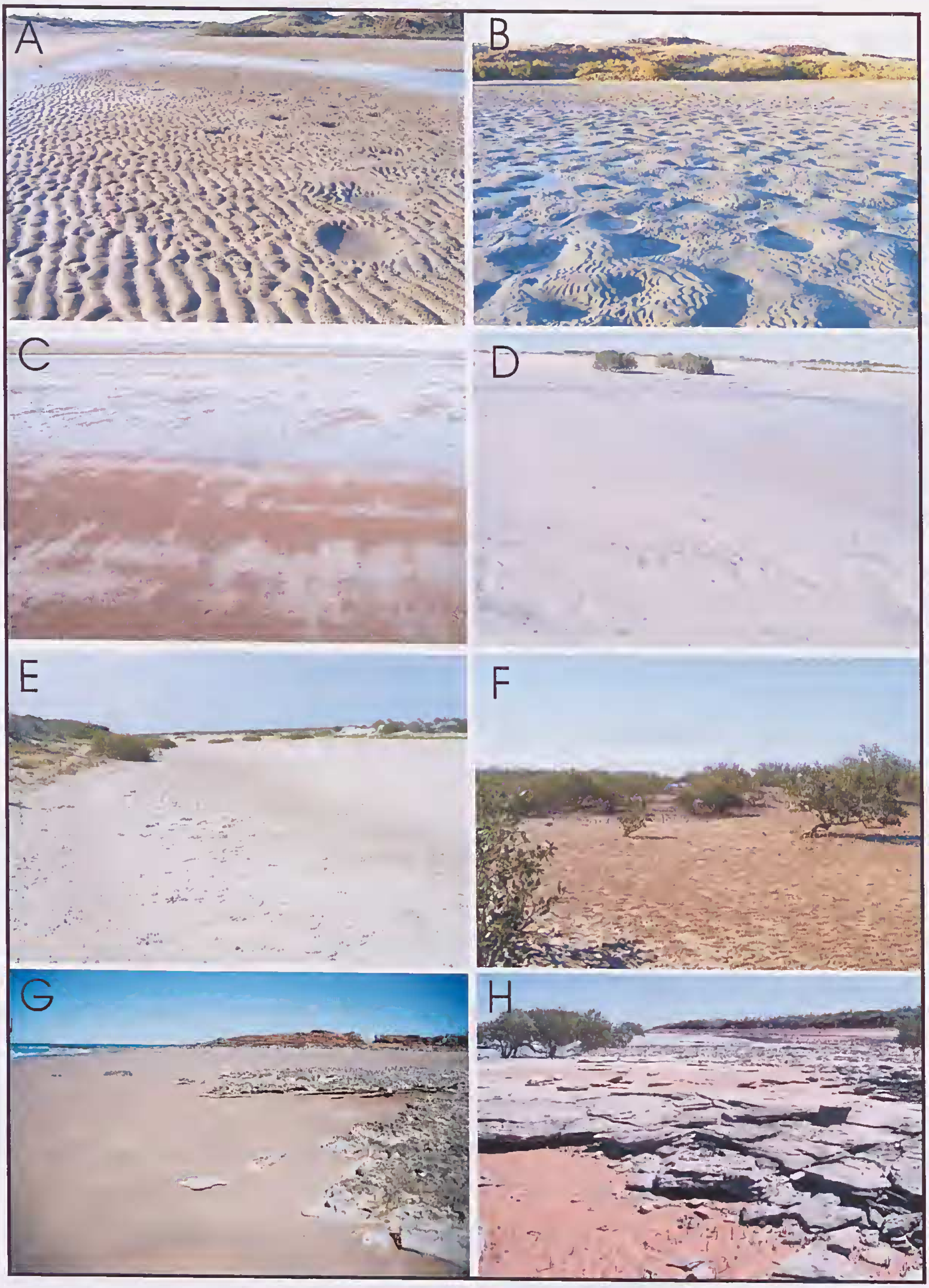

Figure 13. Photographs of soldier crab habitats, and some environmental gradients in the field, ordered from most common to relatively least common habitat. A. Shore-parallel shoals that are soldier crab habitats in Hearsons Cove. B. Shoals as part of an ebb-tidal delta (within the bay) that are soldier crab habitats in King Bay. C. Low gradient beach and shore-parallel shoal complex at Settlers Beach. D. Shoals and channels that are part of an ebb-tidal delta at the mouth of Willie Creek. E. Soldier crab habitat developed across a high-tidal sand-floored lagoon, bordered by limestone and sand ridges at Coconut Well. F. Soldier crab habitat in the interior of an open mangrove formation with sandy floor on the tidal bank of Nine-mile Creek, Port Hedland. G. Soldier crab habitat at Entrance Point, a moderate wave-dominated sandy beach, with local outcrops of Broome Sandstone. H. Soldier crab habitat on sand patches amongst rock pavement of Broome Sandstone at Black Ledge.

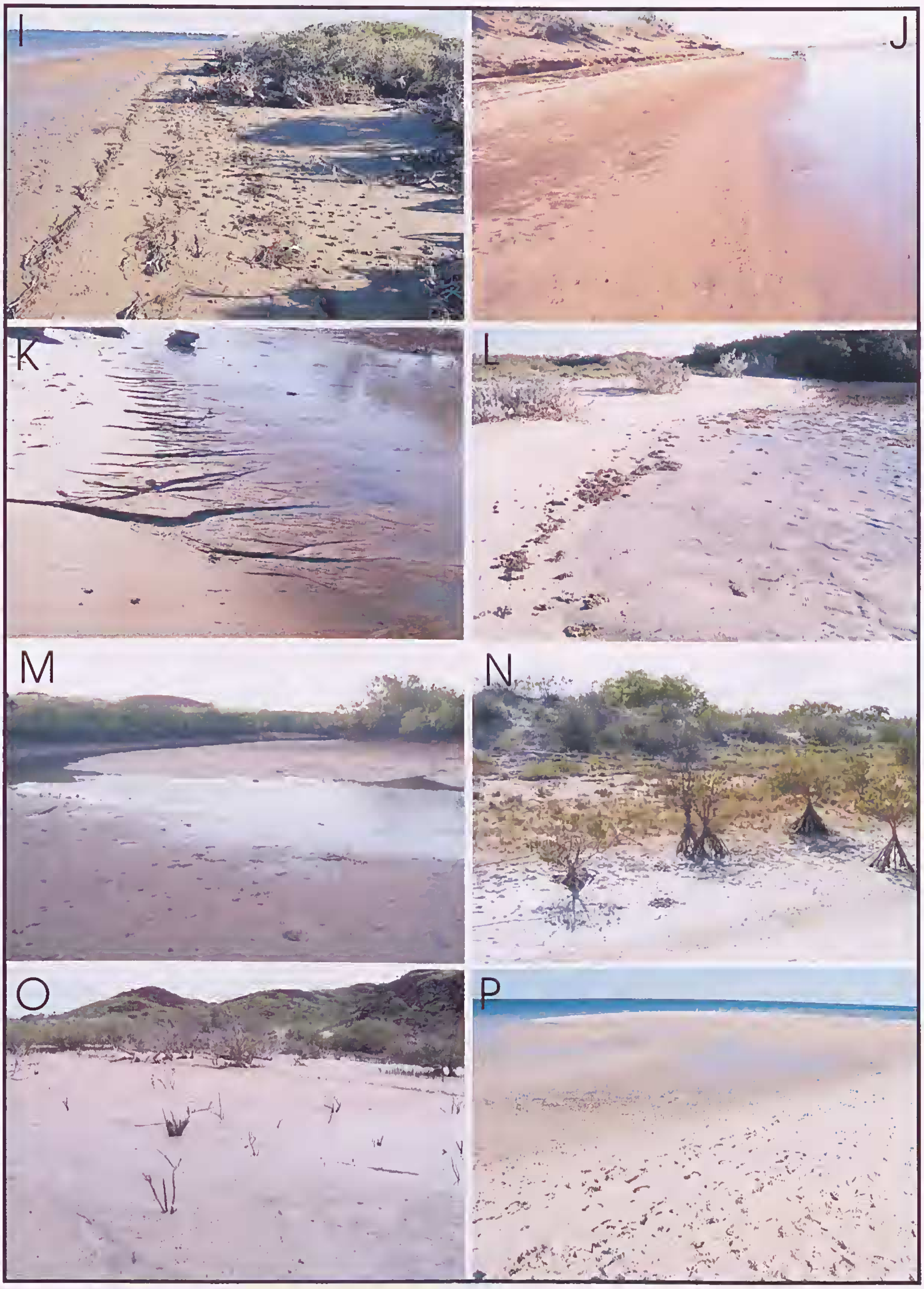

Figure 13 (cont.) I. Shore of the Gascoyne Flats, north-eastern Shark Bay, with narrow ribbon of sand that functions as soldier crab habitat. J. Tidal creek sandy margin that functions as soldier crab habitat at Onslow. K. Marked seepage of seawater from a beach face discharging along the interface between Pleistocene limestone and the beach sand to develop a narrow soldier crab habitat at Six-mile Creek East (also see Fig. 6A). L. Marked seepage of seawater from a beach face discharging along the interface between muddy sand of the low tidal flats and the mid-tidal beach sand to develop a narrow soldier crab habitat at Mangrove Bay, North West Cape (also see Fig. 6B). M. Shoals along the axis of a tidal creek in King Bay that function as a soldier crab habitat. N. The margin of a dune near HAT at Coconut Well, with *Sporobolus virginicus*, *Avicennia marina* and *Ceriops tagal*, and development of a soldier crab habitat. O. Sandy surface of an alluvial fan in the northern part of Hearsons Cove, with soldier crab habitat developed on the sand and amongst the mangroves (in background). P. Sandy spit sheltering a sand-floored depression which functions as soldier crab habitat at Monkey Mia, middle Shark Bay.

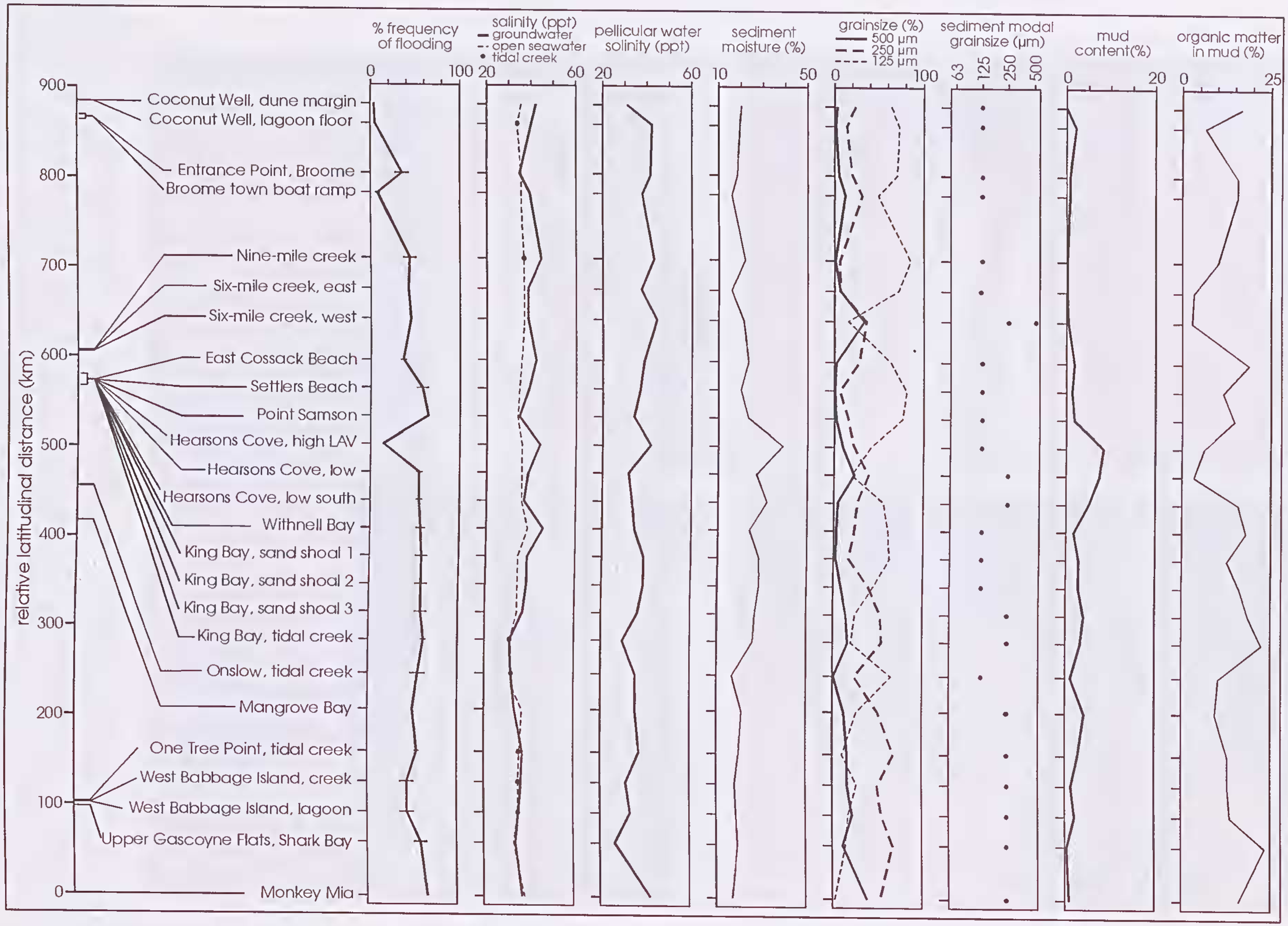

Figure 14. The key abiotic parameters from the twenty-five study sites. The relative latitudinal distance between the sites is shown along the left axis.

Table 9 shows that most soldier crab habitats are mainly located on dissipative shores (particularly those with shoal-and-depression complexes), on sandy substrates (such as shoals and banks) in the wave-protected axes of tidal creeks and on ebb-tidal delta shoals associated with tidal creeks, in tidal lagoons, along the seepage zone at the base of a beach slope, and in high-tidal sandy areas where there is freshwater seepage.

Microtopographic effects

While local factors such as shore slope and depth to groundwater may determine the occurrence of soldier crab habitats within an embayment or along the coast, soldier crabs do not always occur ubiquitously across their habitat on a day-to-day basis. Microtopography within the habitat, which may vary diurnally, is important for determining the diurnal occurrence, distribution, and activity of the crabs at the finer scales by providing suitable moisture conditions for feeding and construction of ichnological structures (such as pustular structures roofing the horizontal tunnels of the crab) during low-tidal periods. Detailed surveying at Sites 13, 15 and 16, in relation to small-scale topography and the water table at low tide, shows that the tidal-flat surface is not always planar, but consists of undulations comprising small-scale mounds and depressions of relative relief of 10–20 (–30) cm, formed as a result of feeding at high tide by demersal fish. A cross-section through the low-relief undulating tidal flat is shown in Figure 15A. Within the microtopographic setting, the water table during low tide was generally consistent in height relative to AHD, but the depth to the water table from the tidal-flat surface varied in relation to the occurrence of mounds or depressions. Some depressions intersected the water table when at low tide and therefore formed "pooled" water. The greatest depth to the water table occurred under the mounds with the highest relief.

The soldier crabs avoided working the surface of areas where mounds were too high (Figure 15B), and the water table at low tide therefore too deep, or where depressions were permanently waterlogged or inundated for that day (Figure 15C). The soldier crabs preferentially occurred on the margins of the higher mounds and over the surface of the medium-sized mounds (Figure 15A). This phenomenon is exemplified best where soldier crabs preferentially pelletised the crest of ripples, showing the extent that depth to a water table and moisture content of sediment played a part in determining crab activity and crab surface occurrences and workings (Figure 15D and 15E). Adults that emerged onto the surface preferentially pelletised the crests of ripples (since ripple crests were elevated above the water table), and pelletised the crests and margins of mounds in the "mound-and-depression" complex.

At Site 15, when the crest of the seaward low-relief shoal that normally did not support populations of soldier crabs (because it was too high above the water table under the tidal flat) was excavated by tidal action over several months to form an intra-shoal depression (15–20 cm deep) on the crest of the shoal, and the shoal surface was brought within 10–15 cm of the water table (at low tide), soldier crabs migrated into that area of the crest of the shoal.

Results of field work to define soldier crab sediment preferences

When the experimental blocks of exotic sediment (mud, muddy sand, grit, and shell fine gravel) were emplaced on the tidal flat at Site 15 to determine what sediments the crabs avoided and what sediments they preferred, the soldier crabs were found to have been migrating throughout the general area by horizontally burrowing, and producing pustular structures (as described by Unno & Semeniuk 2008). The five control sand blocks of natural sediment were inhabited and burrowed by crabs within a day, and these control blocks were constantly burrowed by the crabs over the year. However, the crabs totally avoided from the onset and for the whole year, the mud, muddy sand, shell grit, and shell gravel. A comparison of the grain sizes of the natural sand in the soldier crab habitat and the exotic sediment blocks is illustrated in Figure 10B. This provides an indication of the sediments that soldier crabs avoid.

The granulometry of (soldier crab-free) sediments dominated by gravel-sized and mud-sized fractions that sharply adjoin sandy soldier crab habitats is shown in Figure 10C. This also provided an indication of the sediments that soldier crabs avoided.

Relationship of soldier crabs to mangroves and sea couch

Three sites were studied to specifically to show soldier crab occurrence in relation to mangroves and to sea couch. These field sites were Site 1, Site 5 and Site 10.

At Sites 5 and 10 (Nine-mile Creek, Port Hedland, and Hearsons Cove, Dampier Archipelago, respectively), the occurrence of soldier crabs in relation to the white mangrove (*Avicennia marina*) was investigated. At these sites, even though soldier crabs could inhabit the tidal level where this mangrove grew and, indeed, locally inhabited sandy substrates where the mangrove was open or sparse, there was an absence of soldier crabs where mangroves (and their pneumatophores) were abundant (Figure 16).

At Site 1 (Coconut Well), the occurrence of soldier crabs in relation to sea couch (*Sporobolus virginicus*) was investigated. At this site, even though soldier crabs could inhabit the tidal level where sea couch grew, there was an absence of soldier crabs where sea couch became abundant (Figure 16).

Data analyses: linear regression and Principal Component Analyses

For the linear regressions, all the analyses resulted in low r^2 values (low correlation) and high p-values (poor statistical significance) in testing for a linear relationship between abundance and the other variables. The scatter plots suggest that abundance has neither a linear nor generally monotonic relationship with the other variables. However, there seems to be a non-linear relationship: as abundance values increase, there appears to be an approximate convergence toward the averages of the observed abiotic environmental values. This is consistent with the crabs having an optimum or preferred range of salinity, moisture, mud content, and so on. The

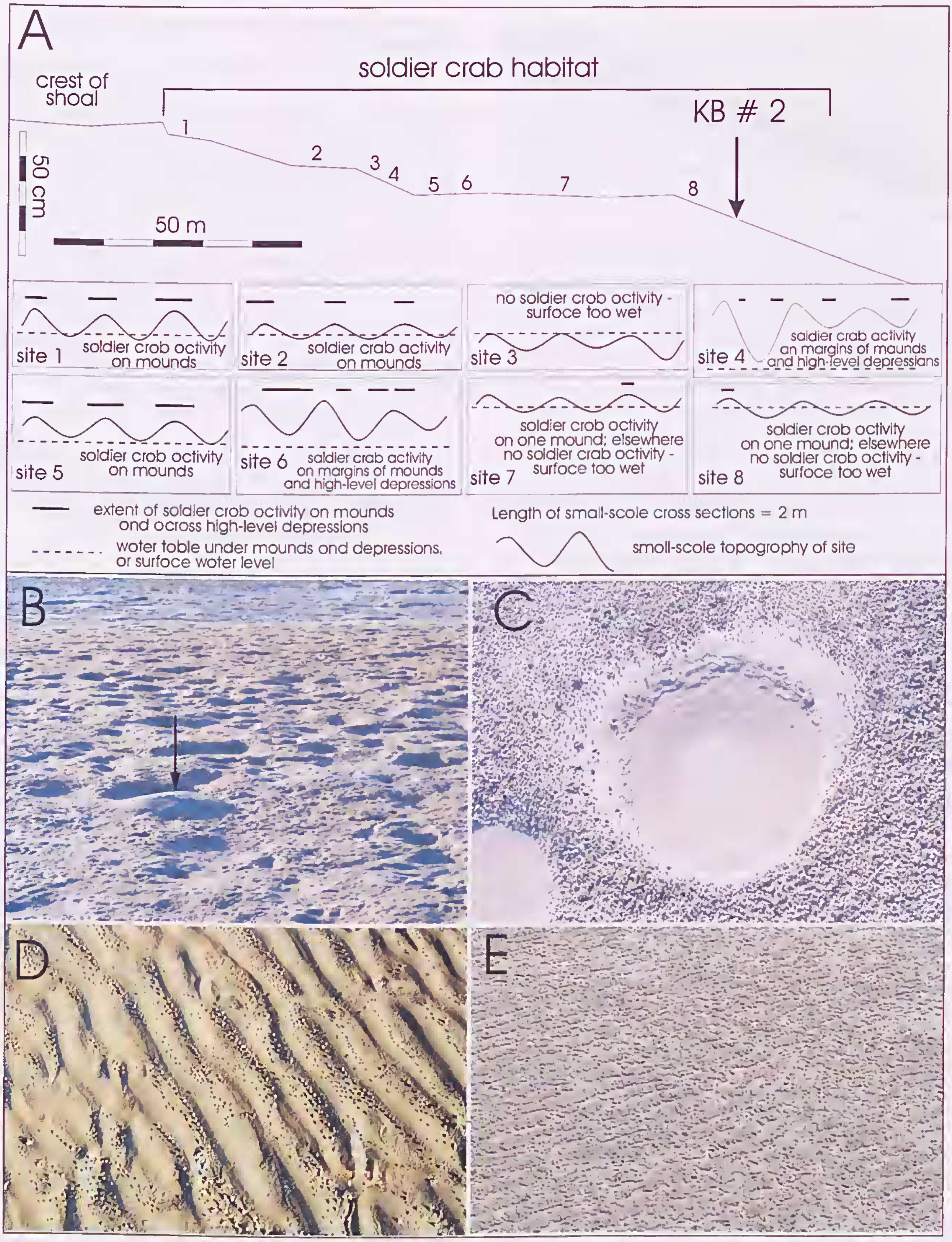

Figure 15. Influence of microtopography on soldier crab occurrence. A. Occurrence of hummocks (mounds) and depressions along a transect on a tidal flat, and detailed topography showing the distribution of crab workings along a hummock and depression in relation to the water table. B. Mound-and-depression complex showing general absence of soldier crab workings on the mounds (one is arrowed). C. Soldier crab workings along the margins of a depression, and their absence in the depression where the substrate was too close to the water table or was inundated. D. Emergent adult crabs have pelletised the tidal flat surface, preferentially working along the crest of ripples. E. Rippled tidal flat where soldier crabs have preferentially pelletised the ripple crests and avoided the inter-ripple troughs.

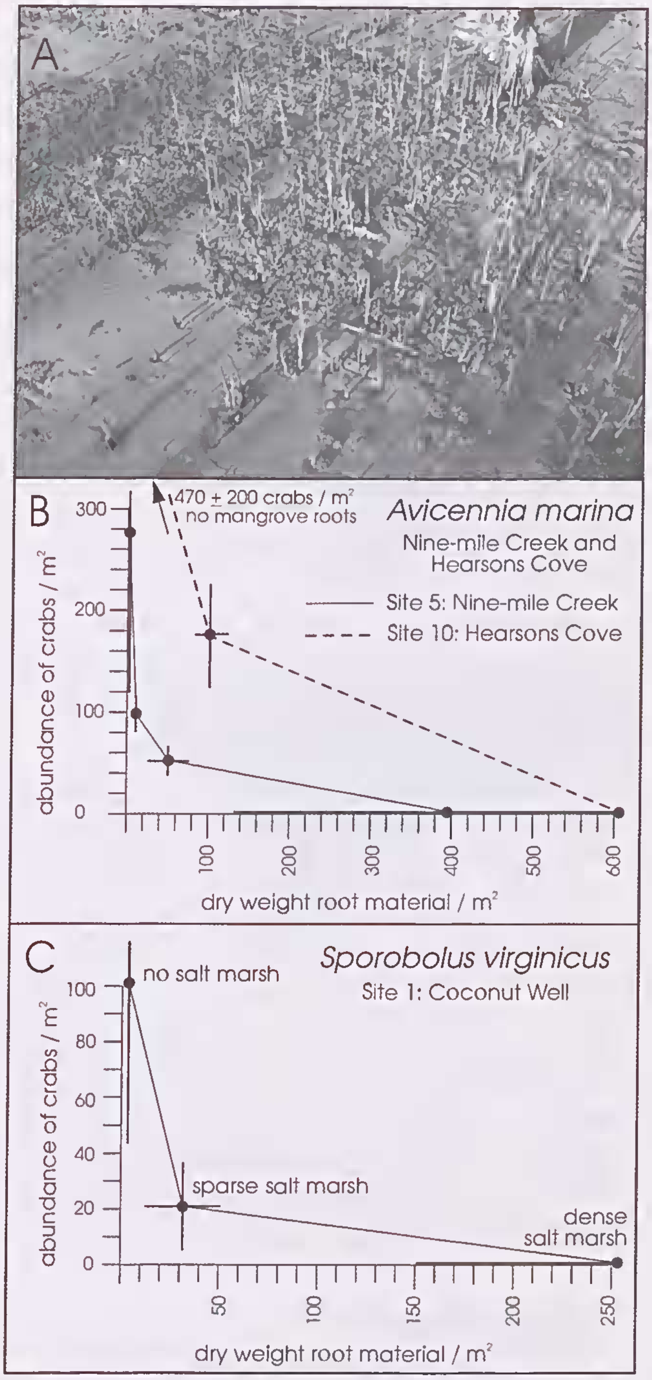

Figure 16. Soldier crabs in relation to mangrove pneumatophores and sea couch. A. Pustular workings amongst the pneumatophores. B. Relationship between crab numbers and mangrove root density. C. Relationship between crab numbers and sea couch root density.

results of the regression analyses are presented in Appendix 2.

Principal Component Analyses using orthogonal (Varimax) and oblique (Direct Oblimin) rotations gave reasonably similar results with no serious conflict of interpretation between them (Appendix 2). Abundance loaded strongly onto the third component, whilst the other variables in the third component have only weak to moderate (linear) association. The third component accounts for only 12.5% to 13.0% of the variance in the original data. Principal Component Analyses show again that abundance has neither a linear nor generally monotonic relationship with the other variables, which is consistent with the crabs having an optimum or preferred range of salinity, moisture, mud content, and so on. The scatter plots reveal that the weak to moderate association with abundance seems due to some environmental data values skewing in relation to the crabs' optimal range.

The Principal Component Analyses showed that, along a given axis, the following abiotic features were strongly inter-related as determinants for soldier crab occurrence: mud content of sediment, and depth to water table at low tide. Along axis 1, pellicular water salinity, sediment moisture content, organic matter in the sediment, mud content, and depth to water table at low tide were associated. Along axis 2, ground water salinity, grain size, and organic matter in the mud fraction were associated. Along axis 3, pellicular water salinity, mud content, organic matter in the mud, and crab abundance were associated. The results from PRIMER 6 corroborated that soldier crab occurrence was related to mud content of sediment, depth to water table at low tide, pellicular water salinity, sediment moisture content, organic matter in the sediment, ground water salinity, sediment grain size, and organic matter in the mud fraction (Appendix 2).

Case studies to illustrate the relationship of the soldier crab habitat to wave energy and other abiotic factors

Cable Beach, Entrance Point, Hearsons Cove and King Bay provide case studies to illustrate the relationship of the soldier crab habitat to wave energy and other abiotic factors. Cable Beach and Entrance Point, at Broome, show a contrast between an exposed beach and a relatively more sheltered beach – soldier crabs are absent from the former, and inhabit the latter. Hearsons Cove, on the south-western shore of Nickol Bay, along the eastern edge of the Burrup "Peninsula"[1] in the Dampier Archipelago, and King Bay along the southeastern margin of the Burrup "Peninsula" provide case studies of seven soldier crab habitats developed in relation to abiotic environmental factors that include wave energy, tidal level, grain size, pellicular water salinity, and fresh-water seepage.

For Hearsons Cove and King Bay, some more specific information on wave energy in the region of the Dampier Archipelago, as background beyond the regional considerations provided earlier, is described below. In terms of wave energy, the Dampier Archipelago is subjected to regional swell and locally-generated wind waves (Figure 17). The swell derives from south-western to western quadrants (originating from the refracted swell from the Southern Ocean and directly from the Indian Ocean), and from eastern quadrants (originating from the Indian Ocean), as described by Semeniuk & Wurm (1987) and Pearce *et al.* (2003). In the Dampier Archipelago, wind waves follow wind directions. Semeniuk & Wurm (1987) summarise the information on the two main seasons of wind direction that generate wind waves significant in coastal processes. Where swell

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[1] the "Burrup Peninsula" is not a true peninsula – it actually is a linear series of rocky islands formerly connected at their southern end by a tidally-flooded, sediment-infilled seaway. Today, it is connected to the mainland by causeways.

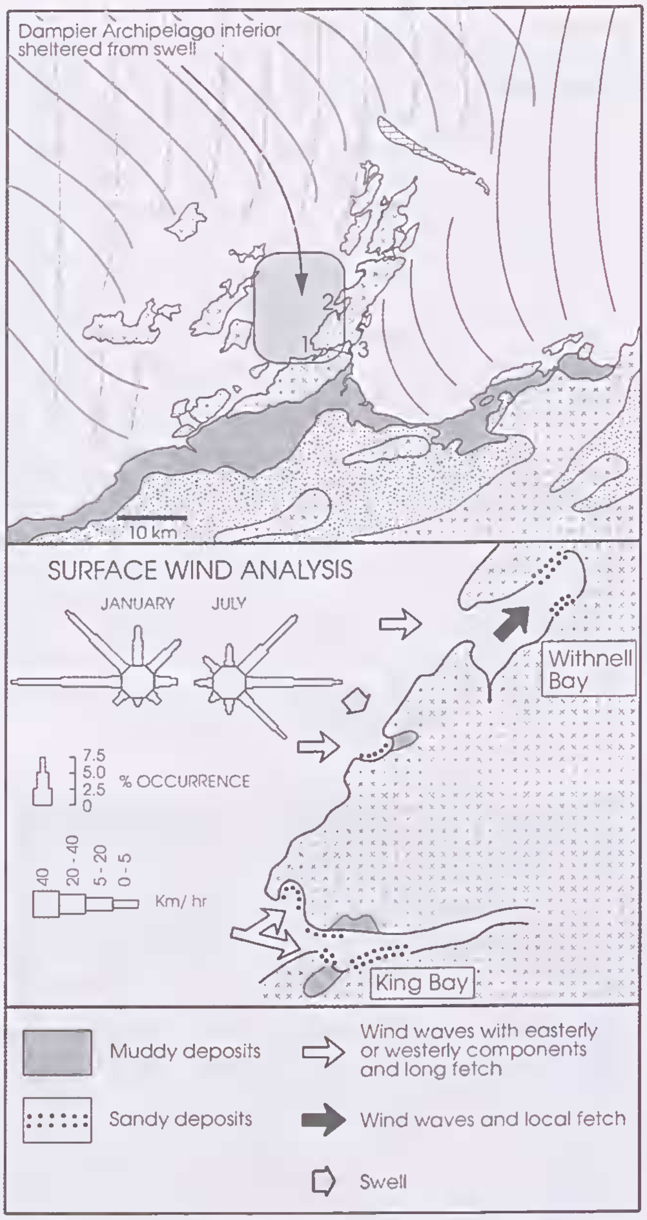


Figure 17. The oceanographic setting of the Dampier Archipelago. A. The refraction of south-westerly, westerly and easterly swell by islands of the archipelago and large bays, the region of eastern Burrup "Peninsula" (circled) that is largely protected from direct impact of swell, and location of King Bay (1), Withnell Bay (2) and Hearsons Cove (3). B. The surface wind patterns that result in wind waves, and the direction of wind waves that impinge on King Bay and Withnell Bay (after Semeniuk & Wurm 1987).

and wind waves directly impinge on the shore, they generate wave-dominated coastal landforms and sedimentary bodies (Semeniuk & Wurm 1987): the coast tends to be wave-washed rocky shores or high-energy beaches, as exemplified by the eastern margin of the Burrup "Peninsula" (Semeniuk *et al.* 1982). Where partly or moderately protected from swell and wind waves, coasts tend to be sandy shores, or sandy tidal flats, and where protected from swell and partly from wind waves, coasts tend to be muddy or muddy-sand tidal flats.

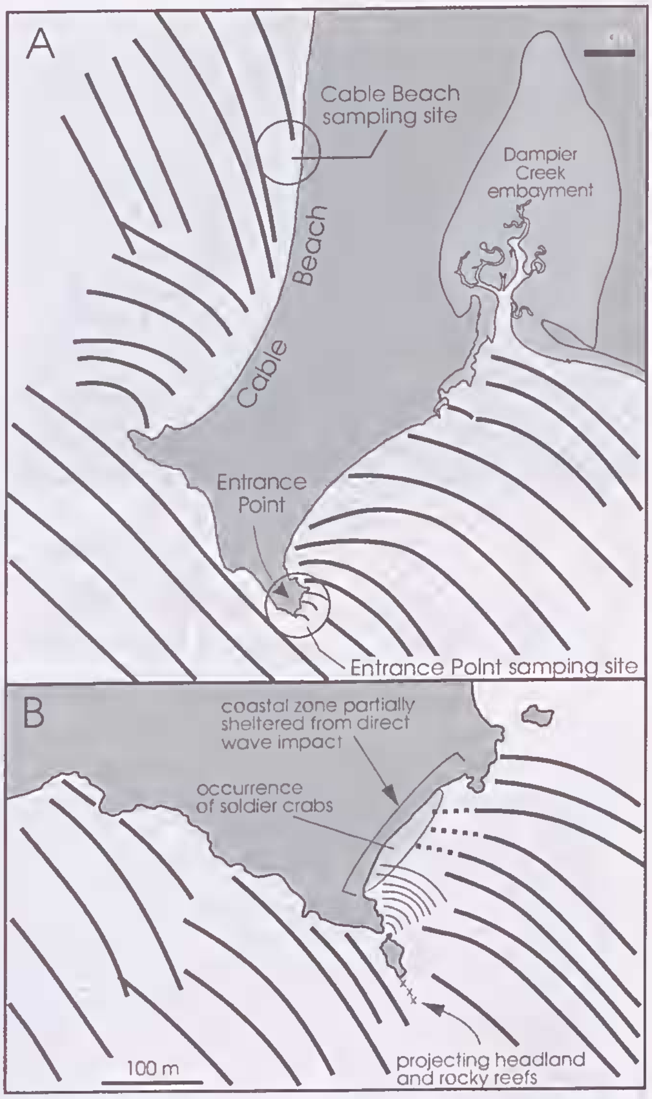


Figure 18. A. Annotated map of the comparative oceanographic, geomorphic and sedimentologic setting of Entrance Point and Cable Beach; soldier crabs occur at Entrance Point but not at Cable Beach. B. More detailed map of Entrance Point showing headland-and-reef topography providing shelter from waves (by refraction), and the location of the soldier crab habitat.

Cable Beach and Entrance Point

Cable Beach and Entrance Point (Site 3 of the regional transect study) are two wave-dominated beaches in the Broome area (Figure 18). Cable Beach is more exposed than Entrance Point in that it more directly faces the swell and wind waves of the Indian Ocean, while Entrance Point is slightly more protected, being leeward of, and semi-sheltered by a ridge of Mesozoic rock, and receives refracted swell and wind waves (Figure 18). Using the criteria to rank exposure/shelter developed by Brown (1990), Cable Beach scores 11 and is graded as exposed, and Entrance Point scores 10, and is graded as sheltered (on the boundary between sheltered and exposed). The two beaches, in close proximity to each other illustrate that for soldier crabs a score of 11 using the criteria of Brown (1990) signals a beach too high in wave energy to support soldier crabs. As such, Cable Beach is too high in wave energy, while Entrance Point is borderline (reflected in the fact that soldier crabs are not abundant at this beach).

Hearsons Cove

As an open embayment, subjected to a graded wave climate along its length (decreasing in wave energy to the north), Hearsons Cove provides an excellent example of the inter-relationship of coastal landforms, sedimentary accumulations, steepness of shore, grain-size distribution in relation to wave energy, and pellicular water content and its water salinity.

Hearsons Cove is a north-south oriented open embayment occurring between two protruding headlands of Precambrian rock, between which there is a curved steep reflective beach located between MSL and HAT that is backed to landward by a shore parallel sand dune. Seaward of the beach is a gently sloping, low-tidal sand flat located between MSL and LAT that is a dissipative shore. The embayment is variably protected along its length from wave action (by refraction and dampening of swell from the eastern quadrants and of wind waves), and as a result there is partitioning of sediment bodies, separation of gravel and sand grain sizes, accumulation of mud (to form muddy sand), and occurrence of mangroves in response to the variable and graded wave energy that impacts on this coast. The southern part of the embayment is subjected to wind waves during all seasons, as well as refracted swell; this segment of the coast is high-energy: it is a wave-washed cliff shore and bouldery shore. At the other extreme, the northern part of the embayment is protected from swell and partly protected from wind waves; this segment of the coast is of a lower energy: it is a fine sand and muddy-sand sedimentary environment which supports mangroves. From south to north, as the wave energy decreases, the grain size along the reflective beach changes progressively (Figure 19): from exposed rock with a thin cover of shell gravel and rock gravel (modal grain size 4000 mm) in the south to coarse sand and finer shell gravel in mid-sections, to medium sand and fine sand (modal grain size 500 mm) in northern sections. The accumulation of fine sand on the low tidal flat in the embayment is asymmetric, with the thicker and wider proportion occurring to the north in the protected zone (Figure 19), effectively in the lee of the northern headland. The mangroves and their associated muddy sand also occur in the most protected part of the embayment.

Within the Cove, with its differential distribution of wave energy, there are three sites for soldier crab habitats, described in order of location in decreasing wave energy (Figure 19):

- Hearsons Cove # 3 – low-tidal, shore-parallel, low-relief shoals in the north-western part of the Cove (*i.e.*, on a shoal complex developed only in the middle to northern parts of the Cove);
- Hearsons Cove # 2 – a low-relief shoal just below MSL, parallel to the front of the mangroves, further in the north-western part of the Cove; and
- Hearsons Cove # 1 – the high-tidal part of an alluvial fan at ~ MHWS, landward of the mangroves in the extreme north-western part of the Cove.

The reflective beach at Hearsons Cove does not provide soldier crab habitats: along the base of the beach slope in the middle to southern parts of the embayment, the sediments are too coarse or too mobile, and in northern parts, where the grain size of the beach is less coarse, the slope is too steep (and freely draining of groundwater during low tide). Hence the combinations of wave energy, grain size, steepness of shore, and pellicular water content and salinity has constrained the crab to inhabit a localised area in front of the reflective beach on shore-parallel shoals, and in front of the mangroves – effectively in that part of the low-tidal sand flat subjected to the lowest level of wave energy. These particular locations highlight the significance of low wave energy in determining soldier crab occurrence, and also the importance of grain size and pellicular water content.

Being below MSL, the habitat at Hearsons Cove # 3 is flooded on all tides, and the groundwater table, being almost always close to the sediment surface, ensures that the sand has a pellicular water content sufficient to support soldier crabs. The pellicular water salinity is similar to that prevailing throughout the region on low-tidal sand flats. Wind-wave energy and tidal currents are sufficient to cause sand rippling, but not to generate megaripples, and there is not enough sand mobility to eliminate soldier crabs.

The most sheltered soldier crab habitat in Hearsons Cove is the high-tidal part of an alluvial fan located landward of high-tidal mangroves (Hearsons Cove # 1) and partly into the landward zone of the mangroves. This occurrence of soldier crabs contrasts with the traditional perception that they are low-tidal flat inhabitants (Cowles 1915, McNeill 1926, and others). This habitat also highlights the significance of low wave energy in determining soldier crab occurrence, the site being the environment most protected from wave action. Additionally, being flooded only on high spring tides, and being a sandy environment, the area normally should have a water table at low tide that falls to a depth of decimetres during neap tides, and (at the landward zone of the mangroves) groundwater salinity and pellicular water salinity normally would be 80–90 ppt (Semeniuk 1983) – however, groundwater salinity and pellicular water salinity have been diluted by fresh-water seepage, and by seawater seepage stored in the landward dunes. As a high-tidal habitat, this location underscores the significance of fresh water and seawater seepage in maintaining pellicular water content, and in diluting normally hypersaline water to allow the soldier crab to inhabit this unusual environment. The site at Hearsons Cove # 1 illustrates that a range of environmental factors can interact to develop habitat for soldier crabs.

A summary of the geomorphic, oceanographic and sedimentologic setting and essential features of Hearsons Cove in generating soldier crab habitats is shown in Figure 19.

King Bay

King Bay is a V-shaped embayment cut into Precambrian rock. It is protected from regional swell by the cluster of islands of the Dampier Archipelago, *viz.*, East Lewis Island, West Lewis Island, Malus Island, Enderby Island, and Rosemary Island (Figure 17). It is subject to local wind waves (Figure 17; and Figure 4 of Semeniuk & Wurm 1987), but wave translation (energy dissipation) across the length of the embayment results in a decrease in energy of the wind waves from its entrance to its head, as reflected in the sediments: sand at

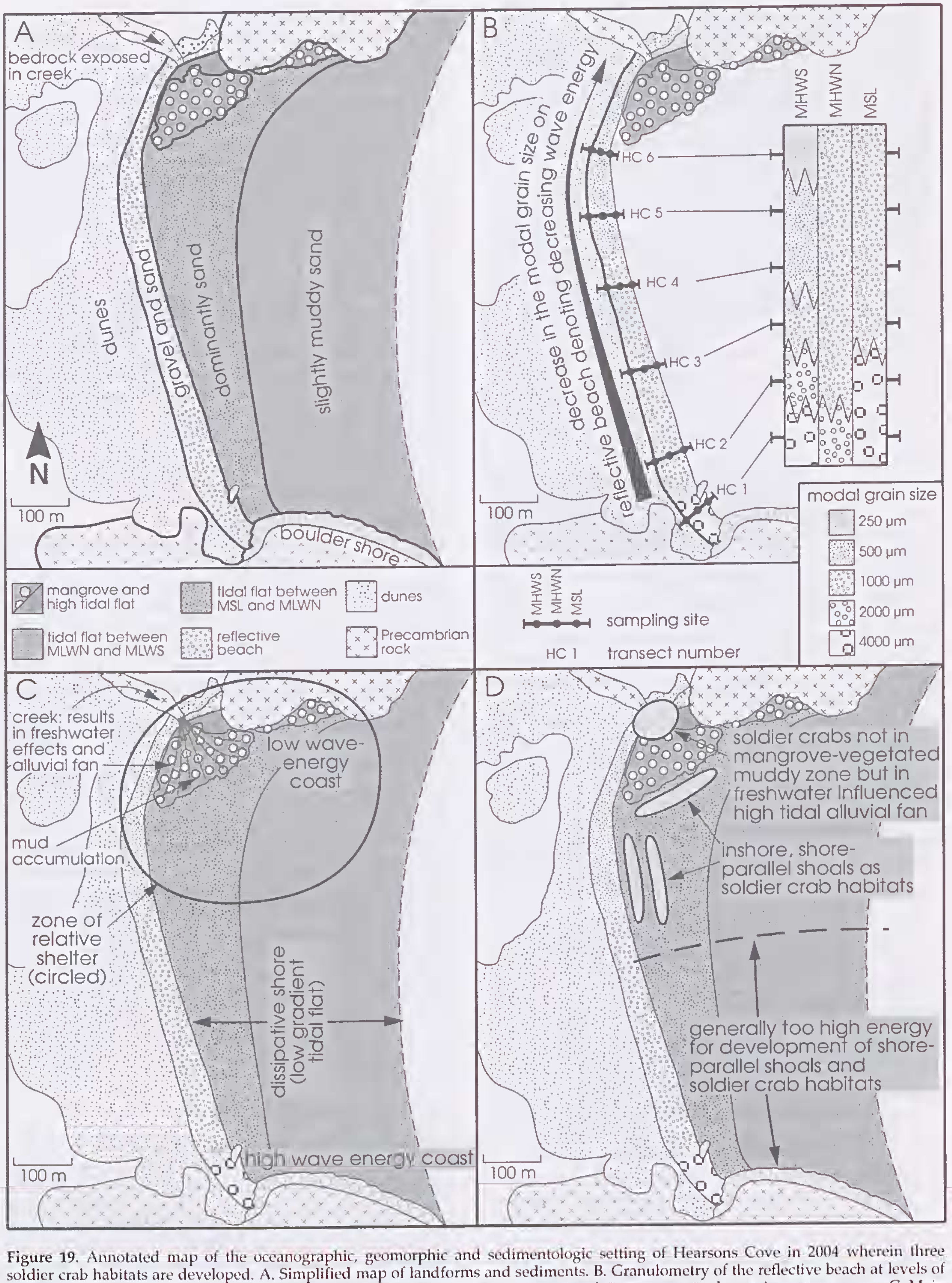


Figure 19. Annotated map of the oceanographic, geomorphic and sedimentologic setting of Hearsons Cove in 2004 wherein three soldier crab habitats are developed. A. Simplified map of landforms and sediments. B. Granulometry of the reflective beach at levels of MSL, MHWN and MHWS showing decrease in modal grain size from south to north in response to decreasing wave energy. C. Main settings and processes leading to zones of relative shelter in the Cove. D. Summary showing location of the soldier crab habitats developed in Hearsons Cove.

the entrance to the embayment, muddy sand in middle tracts of the embayment, and mud at its head (Semeniuk & Wurm 1987). King Bay thus illustrates an example of the relationship of coastal landforms, sedimentary accumulations, and grain-size distribution in relation to wave energy, and pellicular water content and pellicular water salinity. There are four soldier crab habitats, all located between *circa* MSL and MLWN. The King Bay location also highlights the subtleties of wave energy in determining soldier crab occurrence.

There are seven sites that function as soldier crab habitats in King Bay, and all occur in a re-entrant in the southern part of the Bay. The re-entrant is partly protected by a headland of limestone and Precambrian rock. Four of the sites are part of the transects used in this study (*viz.*, King Bay # 1, King Bay # 2, King Bay # 3, and King Bay # 4). In that part of the embayment where local wind-generated wave action is moderate and sand is accumulating, there are two sand shoals (King Bay # 1 and King Bay # 2) formed as part of a sandy ebb-tidal delta, partly anchored by copses of mangroves. Aerial photography shows that the mangrove-vegetated shoals have been in existence for at least 70 years. Soldier crabs have been observed inhabiting the shoals for the past 30 years. The mangrove-vegetated shoals stand some 50 cm above the general level of the tidal flat and are 20–30 m in length and 10 m wide. They form local low-relief "barriers" to the wave energy translating across the tidal flat. Soldier crabs inhabit the leeward side of the two shoals, semi-protected from the wind-waves. In contrast, on the windward side of the western shoal complex nearest to the mouth of the embayment, and in spite of the fact that the tidal levels are the same, there has been an absence of soldier crabs (as observed over 30 years). The critical factor in maintaining these two soldier crab habitats is the subtle protection from wind waves by these shoals and their local mangrove copses. The third soldier crab habitat in King Bay (King Bay # 3) is a shore-parallel linear sand bar, elevated up to 30 cm above the general level of the tidal flat. It is located further into the King Bay embayment, and in the context of wave energy decreasing as it penetrates into the embayment, this site is located in a zone of lower energy than the previous two sites. The linear sand bar is surrounded by muddy sand (too muddy for soldier crab habitation). Even though further into the embayment (and notwithstanding that wave energy is decreasing such that the surrounding environment has become too muddy, with a mud content > 10%), the linear sand bar forms an ideal soldier crab habitat, and being elevated above the general water-saturated tidal flat, it drains such that the groundwater table at low tide is ~ 10 cm below its surface. The fourth soldier crab habitat in King Bay (King Bay # 4) is a series of low-tidal sand shoals and sand waves located in the axis of a tidal creek. The shoals are wholly protected from waves and so are located in a zone of lower energy than the previous three sites.

These soldier crab habitats in King Bay, in a context of differential wave energy, illustrate the principle that to develop a soldier crab habitat there should be enough protection from wave action so as not to mobilise the sand (*i.e.*, so that soldier crabs do not need to deal with a shifting mobile substrate), but enough wave action to winnow out mud to create a sediment with < 10% mud. A summary of the geomorphic, oceanographic and sedimentologic setting and essential features of the King Bay embayment in generating soldier crab habitats is shown in Figure 20.

Discussion

The ensuing discussion generally progresses in a scalar manner for the critical features of the environment, commencing with information on the physiological response and behaviour of the soldier crabs, then explaining their occurrence in specific habitats in the light of the transect studies, and finally explaining their occurrence at the regional scale and their biogeographic distribution.

As noted in the Introduction, other species of *Mictyris* worldwide occur in humid climates and, as such, this presents some difficulties in transferring autoecological and physiological information obtained from these other species to *M. occidentalis*. Some generalised generic information can be used and compared across species (*e.g.*, the seemingly similar burrowing behaviour of *M. occidentalis*, *M. longicarpus*, *M brevidactylus*, and *M. platycheles*, or the osmoregulatory feature of the genus *Mictyris*), but detailed information about the physiological and behavioural characteristics of one species should be applied/compared to others with caution. Thus, for instance, while *M. longicarpus* may be able to tolerate salinity up to 50 ppt as determined by experiments (Barnes 1967), which is not to say that this will determine its habitat setting, there are no comparable data available for *M. occidentalis*; this latter species, occurring in an arid setting, may be able to tolerate higher salinity in an experimental setting than the other species of *Mictyris*.

Since *M. occidentalis* has not been the subject of experimental work dedicated to determining physiological responses, physiological limits, and other behavioural features, our approach to assessing what are the habitat determinants for the species generally was field-based, drawing on the information on habitat characteristics from spatial occurrence of the species, and field sampling to describe the features of the environment in which the species was found, supplemented locally by some field experiments that could provide insights into soldier crab occurrence or distribution. Thus, the study largely was not experimental in design (except for the emplacement of exotic blocks of sediments to determine the sediment preferences of soldier crabs), but rather was documentary.

Prior to discussing general soldier crab physiology, behaviour and habitat requirements, a short discussion on air cavities produced in the subsurface sand by *M. occidentalis* is provided, as these structures provide insight into many aspects of soldier crab autoecology. The air cavity is an essential part of the soldier crab's ichnological constructions (Unno & Semeniuk 2008), and such cavities would not survive continual inundation, nor would they survive reworking by waves or strong tidal currents. The air cavity thus constrains the soldier crab to inhabiting tidal environments (above levels of ~

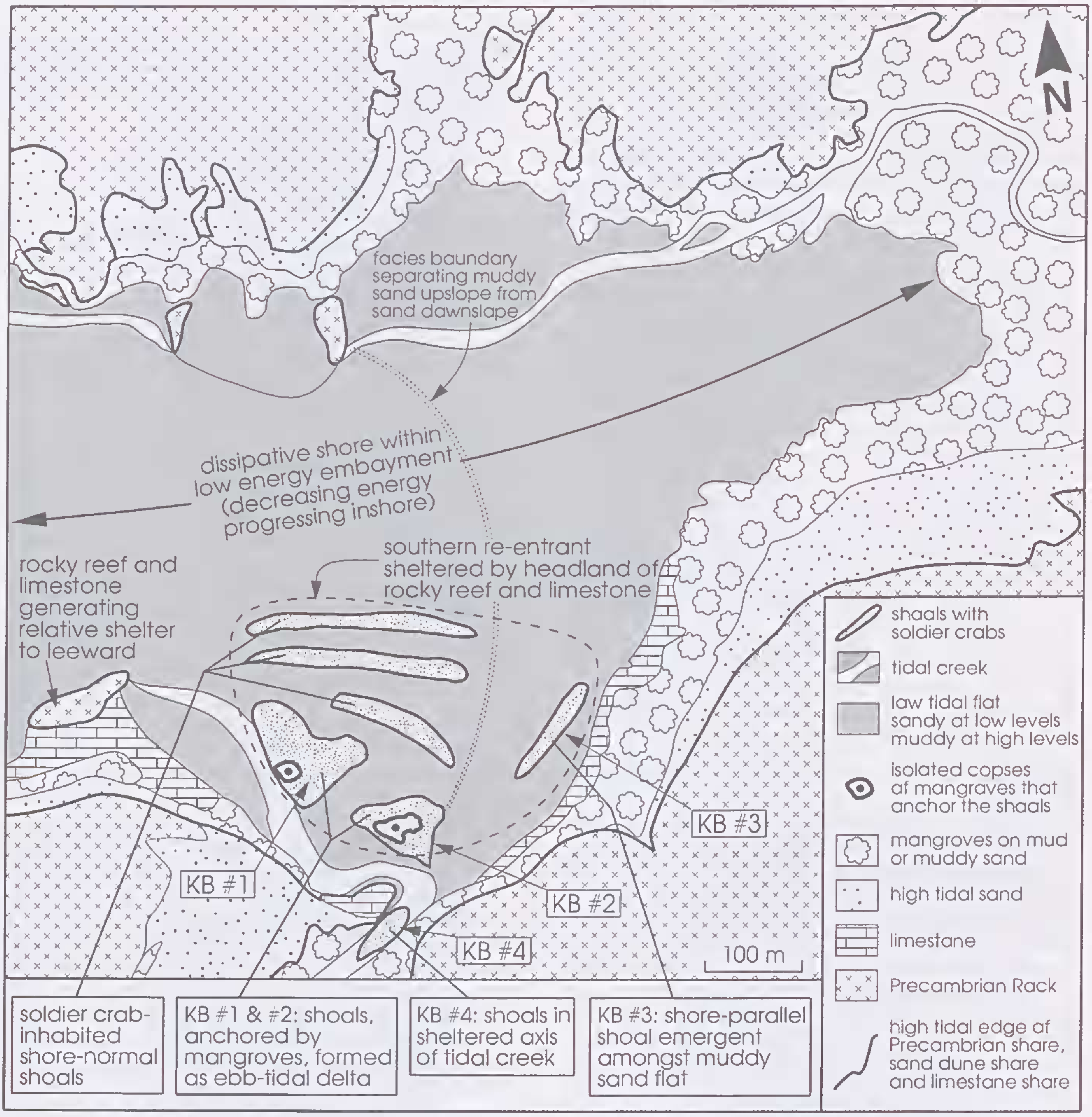


Figure 20. Annotated map of the oceanographic, geomorphic and sedimentologic setting of King Bay in 2004 wherein seven soldier crab habitats are developed, with explanation of the occurrence of the habitats. The soldier crab habitats are discrete shoals in a southern re-entrant of King Bay protected by a low headland Precambrian rock and limestone. This map should be viewed in conjunction with Figure 17B.

MLWN), and inhabiting environments that are not reworked by waves and/or tidal currents to the extent that the upper 10–30 cm of the substrate is mobilised. Tidal levels below MLWN are too frequently inundated, and hence tend to develop the characteristics of subtidal sediments, and the water table at tidal levels of MLWS to LAT tends to be very shallow (< 2 cm) or at the surface, both of which have implications for the soldier crab creating tunnels, or maintaining an air cavity.

Soldier crabs and tidal levels

The soldier crab is not a subtidal brachyuran. It requires exposure during a low tide: firstly, because it largely is a semi-terrestrial brachyuran with well-developed lungs (Maitland 1987; Farrelly & Greenaway 1987; Maitland & Maitland 1992). The soldier crab draws its oxygen predominantly from the air *via* its Milne-Edwards openings, not from oxygen-saturated water. Even though it remains infaunal when the tidal flats are exposed during low tide, enough oxygen can diffuse into the sand interstitially to sustain it; while submerged, it retains an air cavity in which it resides during the high tide, but requires exposure during a low tide to replenish this air cavity. Secondly, it requires being able to swarm at some late stage of its life cycle (Unno & Semeniuk 2008; Unno 2008b). Our observations indicate that the soldier crabs on lower parts of the tidal flat are inundated during the maximum phase of neap tides for two days (of minimal water-level variation, and hence maximum inundation), during which they reside in their subsurface air cavities.

Notwithstanding that *M. occidentalis* is uniquely a species of arid coasts, thus exhibiting anatomical and behavioural characteristics peculiarly adapted to its environmental setting, some discussion is provided here of other species of *Mictyris* in relation to tidal level, even though these other species inhabit coasts of more humid climates. This is on the assumption that some aspects of the genus are generally applicable to all species of *Mictyris*.

There is a generally-held perception that soldier crabs inhabit sandy tidal-flat areas between MSL and low-tide levels, however, very few authors specifically mention tidal levels for *Mictyris*. For instance, McNeill (1926) and other authors just note that the soldier crabs occur on sandy tidal flats, or are intertidal, without referring to the tidal level. There are exceptions: Cowles (1915) noted that *M. brevidactylus* [referred to by Cowles as *M. longicarpus*], was never seen except at low tide and then only at a considerable distance seaward from the high-tide mark on exposed sand flats, but even here there is no precise description of the tidal level that the crab inhabits. Maitland & Maitland (1992), in collecting *M. longicarpus* in the field for their aquarium research, noted that the crabs occurred between neap-tide levels.

This study, regionally, of the soldier crab habitat has shown that *M. occidentalis* can inhabit appropriate tidal areas from levels just below the highest astronomical tide in extreme macrotidal areas to mean low water neap tide (they have not been observed at levels of low-water spring tide). It appears they do not inhabit tidal zones lower than MLWN. There is a reason for this. While soldier crabs occupy air pockets (cavities) during high tide, they cannot stay indefinitely subaqueous and too prolonged an inundation will eventually deprive them of oxygen. From their respiratory requirements and their documented occurrence across tidal flats in north-western Australia, it would appear that the MLWN level is their limit of occurrence in the low-tide direction. That means that their maximum frequency of inundation is ~ 67%.

Moisture and salinity

Soldier crab occurrence is influenced by the pellicular water content (moisture content) of the sediment, and the salinity of groundwater and pellicular water. Since pellicular water is the residual film of water on the sand grains after the tide has ebbed, its salinity develops and increases from/by evaporation during low tide. The salinity of groundwater is important because when the crabs burrow and reside in the subsurface, they may do so in the phreatic zone of the exposed tidal flat, and make direct contact with the saline groundwater. Salinity of groundwater under a tidal flat also is important because capillary rise on low-gradient tidal flats with a shallow water table (at low tide) can moisten the surface to contribute to the pellicular water and to the salinity of the pellicular water. Thus water both remnant from the previous tidal flooding (and circumferential to the sand grains) and the water deriving from capillary rise contribute to the pellicular water on the tidal flat and its salinity.

During a low tide, after marine waters have ebbed off the tidal flat, the groundwater underlying the surface discharges downwards and seawards sympathetically with the fall in the (open) water level, with the result that there is a fall in the groundwater table under the tidal flat. During a spring tide, under sandy substrates at the level of the low-water neap, during a low tide the water table falls by 10–30 cm, leaving an under-saturated zone of damp sand (equivalent to a terrestrial vadose zone), with pellicular water immediately under the tidal-flat surface. This under-saturated zone is where the soldier crabs can build horizontal tunnels roofed by discard pellets (pustular structures) that will not collapse. The surface of the tidal flat lower than levels of mean spring-tide does not sufficiently drain to be effectively used by soldier crabs. In general, the water table at low tide here falls to levels < 10 cm below the surface, or remains at the surface, and the construction of horizontal tunnels roofed by discard pellets will fail because the sand is too water-saturated. There needs to be a degree of drying out of the tidal-flat sand that is required for the successful construction of horizontal tunnels roofed by coherent discard pellets. In this context, very low gradient tidal flats that are poorly draining, with a water table at the surface during low tide, ***i.e.***, saturated (or wet) tidal flats) tend not to support soldier crabs. On the other hand, tidal flats with shoals (in shoal-and-depression complexes) tend to be soldier crabs habitats because the shoals are freely draining because of their relative relief above the surrounding tidal flat.

The upper tidal limit for the occurrence of soldier crabs is determined by a range of factors, including salinity and sediment moisture content. High salinities adversely impact the soldier crab osmoregulatory ability (Barnes 1967). Sand that is too dry, *i.e.*, with low pellicular water content, affects the soldier crab filtration-feeding process (Quinn 1983), and prevents tunnelling and pelletising. In their habitat, soldier crabs have not been found in sediments with pellicular water salinity greater than ~ 44 ppt, or with groundwater salinity greater than ~ 45 ppt, and require a pellicular water content of > 16 %. Where soldier crabs inhabit high-tidal sites (*viz.*, Site 1 and Site 12), where normally high-tide conditions result in hypersaline groundwater and pellicular water (> 50 ppt, and locally in excess of 150 ppt; *cf.* Semeniuk 1983), the conditions of lower groundwater and pellicular water salinity and sediment moisture content conducive to developing soldier crab habitats result from fresh-water seepage or marine water seepage diluting the hypersalinity and increasing the sediment moisture content.

Across sand flats, salinity and pellicular water content change with decreasing inundation and increasing evaporation, factors that will eliminate the crabs. As a result, soldier crabs are eliminated from high-tidal environments by "saline and dry" conditions. However, high-tidal environments can support soldier crabs if the "saline and dry" conditions can be ameliorated by fresh-water seepages and seawater seepages. In these cases, soldier crabs can occur at the levels of the highest tide.

Substrate requirements of the soldier crabs

Given that the Western Australian soldier crab can inhabit tidal environments from low-water neap-tide levels to high-water spring-tide levels, and occur in groundwaters and pellicular waters of salinity 27–45 ppt, the questions arises as to what other abiotic factors determine or constrain their occurrence. Since there is a plethora of tidal habitats situated between MLWN and ~ HAT whereon they could inhabit, the answer lies in understanding the anatomy of the soldier crab, some of its physiological requirements, and its behaviour.

Features of the soldier crab such as its circular body, slender legs, and rotational burrowing indicate that these crabs have developed anatomy and behaviour adapted to inhabiting predominately sandy substrates (to slightly muddy sandy substrates) rather than a mud-dominated substrate such as occurs under mangroves. Some mud content in the substrate may be necessary to retain organic matter for their feeding.

In this study, soldier crabs appeared to prefer a specific grain size of fine to medium sand, varying to a mixture of medium and some coarse sand, and sediment with a mud content of < 8%, though generally with < 1% to ~ 5% mud. Mineralogical composition of sand appears to make no difference to soldier crab occurrence.

There are three lines of evidence that indicate the sediment size range that soldier crabs prefer or avoid. These are:

1 sediment samples from the twenty-five transects of the soldier crab habitat were a medium to fine sand with the mud content mostly ~ 0.5 % to ~ 5%;

2 soldier crabs, in feeding in their natural environment (either in the subsurface in their horizontal tunnels, or on the surface to produce discard pellets; *cf.* Unno & Semeniuk 2008) do not feed from mud or coarse sand, shell grit, or gravel, as they cannot produce within their buccal cavity from such sediments the slurry from which they extract their food (and then discard as pellets); as a consequence, from a sediment perspective, soldier crabs are not found on muddy tidal flats, muddy mangrove-vegetated flats, shell grit or shell gravel substrates, or rocky shores; and

3 the experimental blocks of exotic and natural sediments showed that the crabs totally avoided the mud, muddy sand, shell grit, and fine shell gravel for the whole year, but very quickly inhabited the locally-occurring (initially crab-free) sediment.

In mixed sand-and-mud tide-dominated systems, tidal level and wave and tide processes produce a gradient of sand to mud from low tide to high tide, with mud content generally increasing upslope on the tidal flat (Postma 1961; Semeniuk 1981, 2005). The increase in mud content upslope will determine where soldier crabs occur along the tidal gradient. Within the framework of coastal forms presented in Figure 5, the preferred location of soldier crab habitats in sand-dominated systems and sand-and-mud-dominated systems is shown in Figure 21. On sandy wave-dominated shores that are partly wave-reflective and partly wave-dissipative, muddy sediment tends to accumulate on low tidal flats and in the subtidal environment.

Soldier crabs, mangroves and salt marsh

Soldier crabs can inhabit zones of open mangrove shrub, or mangroves formations with partially closed canopy, as long as the substrate is sandy, has minimal mud, appropriate moisture levels and groundwater and pellicular water salinity, and is able to be burrowed between any pneumatophores, cable roots and root hairs. This observation was one of the unexpected outcomes of the regional surveys, as traditionally, soldier crabs are viewed as inhabitants of low tidal flats, and generally are not associated with the interior or margins of mangrove environments.

In the high-tidal zones, near levels of HAT, if the sandy substrate, moisture levels, and salinity are appropriate, soldier crabs also can inhabit zones of the sea couch *Sporobolus virginicus*, if the grass is not too dense.

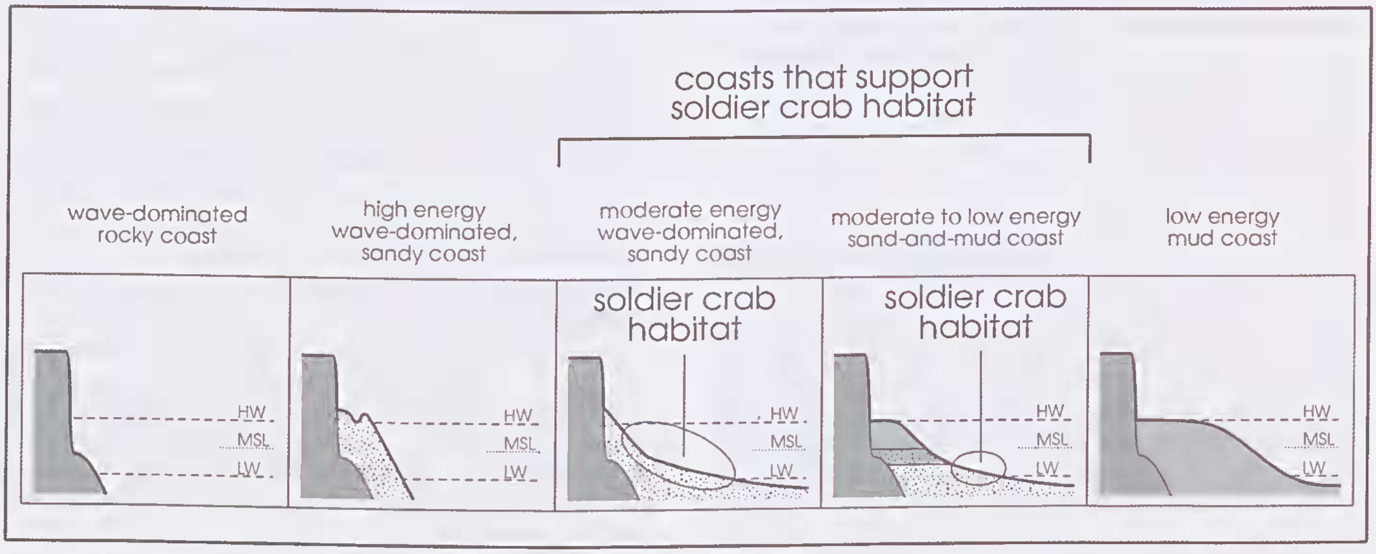


Figure 21. Soldier crab occurrence along the different shores shown in Figure 5.

Habitat requirements of the soldier crab

In its habitat, the soldier crab in Western Australia requires a number of conditions: 1. a sandy substrate within which they can create cavities; 2. a sand that drains of water at low tide, retaining sufficient pellicular water so that the crabs can burrow horizontally, creating a pelletised roof that will not collapse; 3. a sand that is wet enough to extract food particles by micro-slurrying; 4. sand with enough organic matter of mud-sized grade for the latter to be a viable food source; 5. sand with a low enough content of mud-sized mineral matter so that interstitial water can readily flow, entraining food particles, into the subsurface cavities when the crabs are submerged (see Figure 10B of Unno & Semeniuk 2008); 6. when the crabs are emergent, sand that can readily be harvested into the buccal cavity from the damp surface to extract the pellicular water and its entrained mud-and-organic-matter slurry (a higher mineral-matter mud content, and in particular, mud comprised of clay-sized phyllosilicates would result in bonding of water onto the clay particles); 7. groundwater and pellicular water of sufficiently (relative) low salinity so as not to physiologically stress the crab (*i.e.*, < 45 ppt); and 8. sand that is not extremely mobile.

High-energy, wave-dominated environments, or macrotidal environments where megaripples are mobile, as well as creating a relatively unstable substrate where the subsurface cavities of the crabs would not survive, would winnow the sand free of any mud and its fine-grained, organic matter. Furthermore, a mobile megarippled system, with a megaripple height of 10–20 (to 30 cm) , whether generated by wave action or by tidal currents, would mobilise the sand to that depth and hence entrain any soldier crab inhabiting the 0–15 cm depth interval into the dynamic sand, and in the process, destroy their air cavity. Thus, on wave-energy and tidal-energy considerations, megarippled sand is not a soldier crab habitat.

These requirements eliminate, therefore, the following environments as possible soldier crab habitats:

1 rocky shores and bouldery shores, axiomatically, because there is nowhere to burrow and no food source to pelletise;

2 steep sandy beaches between MSL and HWS, because such beaches drain tidal groundwater so rapidly that the environment becomes too dry for the crabs, and the pellicular water of the environment commonly becomes too saline;

3 muddy environments because there is not the opportunity to micro-slurry the surface sediment into pellets to extract food particles;

4 dense mangrove-vegetated environments with muddy substrates because there is not the opportunity to micro-slurry the surface sediment into pellets to extract food particles;

5 dense mangrove-vegetated environments and salt marsh environments with sandy substrates because the abundant roots and root hairs hinder horizontal burrowing;

6 high-tidal sand flats, without fresh-water seepage, because the groundwater and pellicular water are too saline, and the substrates become too dry during neap tides;

7 all strongly wave-agitated and tidally-dynamic sandy environments because the sand is mobile to depths varying from several centimetres to decimetres, with development of plane beds and megaripples which disrupt the air cavities of the crabs; in such environments the crabs would have to spend the high tide buried in sand without an air pocket (effectively being placed in the equivalent of a subtidal environment); and

8 low-tidal sand flats below MLWN that are permanently waterlogged (with a very shallow water table at low tide), as at low spring tidal level; such flats do not allow the crabs to build pellet-roofed horizontal tunnels, and being too waterlogged, these types of structures would collapse.

Against the backdrop of the range of pellicular water content, pellicular water salinity, and groundwater salinity that *M. occidentalis* can tolerate, summarised earlier, the requirements of the Western Australian solder crab result in the following environments as habitats:

1 relatively low-energy, sandy low-tidal flats of fine-medium sand, between MSL and LWN, where the tidal groundwater table falls to ~ 10–20 cm deep;

2 relatively low-energy, sandy high-tidal flats of fine-medium sand, between MSL and HWN, where the tidal groundwater table falls to ~ 10–20 cm deep and groundwater and pellicular water salinity, and pellicular water content are maintained because of fresh water and seawater seepage;

3 relatively low-energy, sandy high-tidal flats of fine-medium sand, between HWN and HWS, where the tidal groundwater table falls to < 10 cm deep, and groundwater and pellicular water salinity, and pellicular water content are maintained because of fresh water and seawater seepage;

4 relatively low-energy, sandy, high-tidal sand slopes of fine-medium sand, at ~ HAT, where groundwater and pellicular water salinity, and pellicular water content are maintained because of fresh-water seepage;

5 moderate-energy, sandy tidal sand flats of fine-medium sand, seaward of steep sandy beaches at ~ MSL where groundwater and pellicular water salinity, and pellicular water content are maintained because of seawater seepage from the beach face into the base of the beach slope;

6 moderate-energy, lower part of a sandy beach at ~ MSL where groundwater and pellicular water salinity, and pellicular water content are maintained because of seawater seepage from the beach face into the base of the beach slope;

7 moderate-energy, low-gradient beach of fine-medium sand, at ~ MSL to MLWN where groundwater and pellicular water salinity, and pellicular water content are maintained because of seawater seepage from higher on the beach face

(the upper slope of the beach does not receive such prevailing seawater seepage and dries out);

8 low-energy, low-gradient shores of fine-medium sand, at ~ MSL to MHWS, adjacent to or within zones of mangroves, particularly where groundwater and pellicular water salinity, and pellicular water content are maintained because of fresh-water seepage.

The partitioning of the shore profile in mesotidal and macrotidal settings into reflective (relatively steep) beach and dissipative (low gradient) shore is an important one in the development of soldier crab habitats. The configuration of the slopes, as a response to the development of a wave-reflective shore and a wave-dissipative shore, the sediment types therein responding to the wave energy, and hydrological storage and discharge (leading to varying degrees of seawater discharge from the beach face) develops two soldier crab habitats. The zone of seawater discharge at the base of the steep beach face has the potential to develop a narrow habitat for the soldier crab, either immediately at the base of the slope, or in the low tidal flat immediately adjoining it (the upper, more steeply inclined, more wave-agitated zone of the beach slope will be coarser in sand grade and steeper in gradient and subject to greater groundwater discharge and water table fall, and hence will not be the preferred habitat for the soldier crab). Aside from the effects of the seawater discharge from the beach face, the low-gradient shore seaward of it may be a relatively lower wave-energy zone, comprised of a shoal-and-depression complex wherein there will be local shoals and depressions which develop habitats for soldier crabs. Thus the low-gradient dissipative shore seaward of the reflective beach with shoals and depressions will be another preferred habitat for the soldier crab.

In summary, for soldier crabs, high-energy coasts tend to be winnowed free of sediment, and hence are too rocky, or if sand-dominated, the sediment is too mobile. At the other extreme, low-energy coasts tend to be too muddy. Coasts of intermediate-energy settings comprise low-gradient sand flats, or sand-and-mud environments. The sand substrates or the slightly muddy sand substrates of such coasts are the preferred habitat of the soldier crab. However, it is important to note that low gradient flats, particularly in microtidal settings, even if sandy, do not readily drain of tidal waters, and tend to be water-saturated at low tide (wet flats) – these also are not preferred soldier crab habitats.

While extensive tracts of open rocky or a sandy coasts may be of a high-energy nature and generally depauperate of appropriate habitats, some soldier crab habitats may be developed in very localised, low-energy, sheltered environments therein, such as embayments, lagoons, tidal creeks, or the interior of strand plains. This leads on to an explanation of the distribution of soldier crabs along the Western Australian coast.

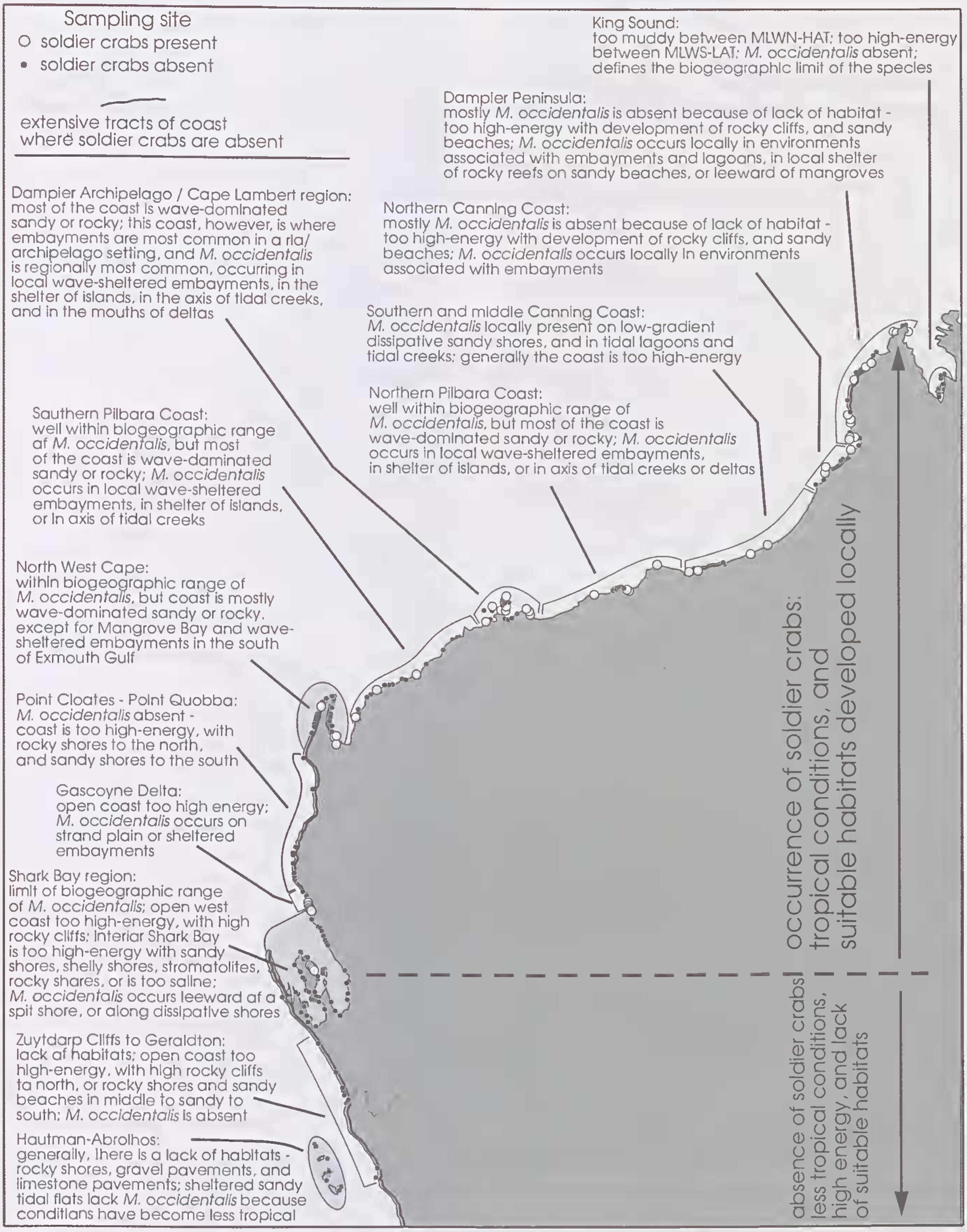
Distribution of habitats and soldier crabs along the Western Australian coast

There are several factors working in conjunction that determine the regional occurrence of soldier crab habitats, and soldier crabs themselves, along the north-western Australian coast; these are: wave energy, coastal type, sedimentary regime, and temperature. Factors determining the regional occurrence of *M. occidentalis* in Western Australia as related to each of the coastal tracts delineated in Figure 8 are summarised in Figure 22.

The northern biogeographic boundary of the Western Australian soldier crab is abrupt, delineated by King Sound. As noted earlier, the tidal flats therein are mud-dominated from levels of MLWN to HAT, and the low tidal flats, where dominated by sand, are extremely mobile, with dynamic megaripples that rework the substrate daily on spring tides to depths sufficient to eliminate soldier crab habitats. Thus, as extensive as it is, King Sound, as a tidally high-energy, sand-and-mud system, is largely not an area for the development of soldier crab habitats, and forms a natural sedimentological barrier to the northern occurrence of *M. occidentalis*. Another species of *Mictyris* occurs at the north-eastern extremity of King Sound (at Shirley Island; see Figure 2), and extends across the Kimberley Coast into the Northern Territory.

The southern biogeographic boundary of the Western Australian soldier crab in the Monkey Mia area also is relatively sharp. The general absence of the soldier crab within the Shark Bay region outside of the Monkey Mia area appears to be determined by habitat availability and temperature, and provides interesting insights into the determinants for soldier crab occurrence. Several environmental factors combine to exclude soldier crabs over much of Shark Bay; these are: wave-energy conditions, sandy sediment grain size, mud content of sediment, development of algal mats linked to salinity, development of shell pavements, water-saturated conditions on low-gradient tidal flats, salinity, and sea temperatures.

While lack of shelter, poor drainage and unsuitable sediment grain size exclude the occurrence of soldier crabs in most of the Shark Bay coastal habitats, as described earlier, regional sea-temperatures may also have an effect. Temperature is known to limit activity for *M. longicarpus* (Kelemec 1979), and if such experimental information can be applied to *M. occidentalis*, then it follows that temperature can be a regionally-limiting factor. Satellite thermal imagery produced by the National Oceanic and Atmospheric Administration (NOAA) shows, at times, differences in sea surface temperatures between Freycinet Reach to the west and Hopeless Reach to the east, with the eastern area generally being warmer. This difference is caused by an intrusion of warmer water from the southward-trending Leeuwin Current that in winter appears to impinge on the north-eastern coast of Peron Peninsula, including the Monkey Mia area. The warmer water generally does not fully penetrate into the southern parts of Shark Bay as far as Hamelin Pool. This limited warm water intrusion into Hopeless Reach may explain the local occurrence of *M. occidentalis* in the Monkey Mia area, and even though such warm water occasionally may penetrate into Hopeless Reach further south than the Monkey Mia area itself, there are no suitable substrates for soldier crabs to inhabit. Warm water also may penetrate into the northern parts of Freycinet Reach but, again, there are no suitable substrates for soldier crabs to inhabit.



King Sound: too muddy between MLWN-HAT; too high-energy between MLWS-LAT; *M. occidentalis* absent; defines the biogeographic limit of the species

Dampier Peninsula: mostly *M. occidentalis* is absent because of lack of habitat - too high-energy with development of rocky cliffs, and sandy beaches; *M. occidentalis* occurs locally in environments associated with embayments and lagoons, in local shelter of rocky reefs on sandy beaches, or leeward of mangroves

Dampier Archipelago / Cape Lambert region: most of the coast is wave-dominated sandy or rocky; this coast, however, is where embayments are most common in a ria/archipelago setting, and *M. occidentalis* is regionally most common, occurring in local wave-sheltered embayments, in the shelter of islands, in the axis of tidal creeks, and in the mouths of deltas

Northern Canning Coast: mostly *M. occidentalis* is absent because of lack of habitat - too high-energy with development of rocky cliffs, and sandy beaches; *M. occidentalis* occurs locally in environments associated with embayments

Southern and middle Canning Coast: *M. occidentalis* locally present on low-gradient dissipative sandy shores, and in tidal lagoons and tidal creeks; generally the coast is too high-energy

Northern Pilbara Coast: well within biogeographic range of *M. occidentalis*, but most of the coast is wave-dominated sandy or rocky; *M. occidentalis* occurs in local wave-sheltered embayments, in shelter of islands, or in axis of tidal creeks or deltas

Southern Pilbara Coast: well within biogeographic range of *M. occidentalis*, but most of the coast is wave-dominated sandy or rocky; *M. occidentalis* occurs in local wave-sheltered embayments, in shelter of islands, or in axis of tidal creeks

North West Cape: within biogeographic range of *M. occidentalis*, but coast is mostly wave-dominated sandy or rocky, except for Mangrove Bay and wave-sheltered embayments in the south of Exmouth Gulf

Point Cloates - Point Quobba: *M. occidentalis* absent - coast is too high-energy, with rocky shores to the north, and sandy shores to the south

Gascoyne Delta: open coast too high energy; *M. occidentalis* occurs on strand plain or sheltered embayments

Shark Bay region: limit of biogeographic range of *M. occidentalis*; open west coast too high-energy, with high rocky cliffs; interior Shark Bay is too high-energy with sandy shores, shelly shores, stromatolites, rocky shores, or is too saline; *M. occidentalis* occurs leeward of a spit shore, or along dissipative shores

Zuytdorp Cliffs to Geraldton: lack of habitats; open coast too high-energy, with high rocky cliffs to north, or rocky shores and sandy beaches in middle to sandy to south; *M. occidentalis* is absent

Hautman-Abrolhos: generally, there is a lack of habitats - rocky shores, gravel pavements, and limestone pavements; sheltered sandy tidal flats lack *M. occidentalis* because conditions have become less tropical

Figure 22. The presence and absence of soldier crab habitats and soldier crab occurrence within the biogeographic range of *Mictyris occidentalis* explained in terms of wave energy, coastal types and shore types, substrates, and salinity.

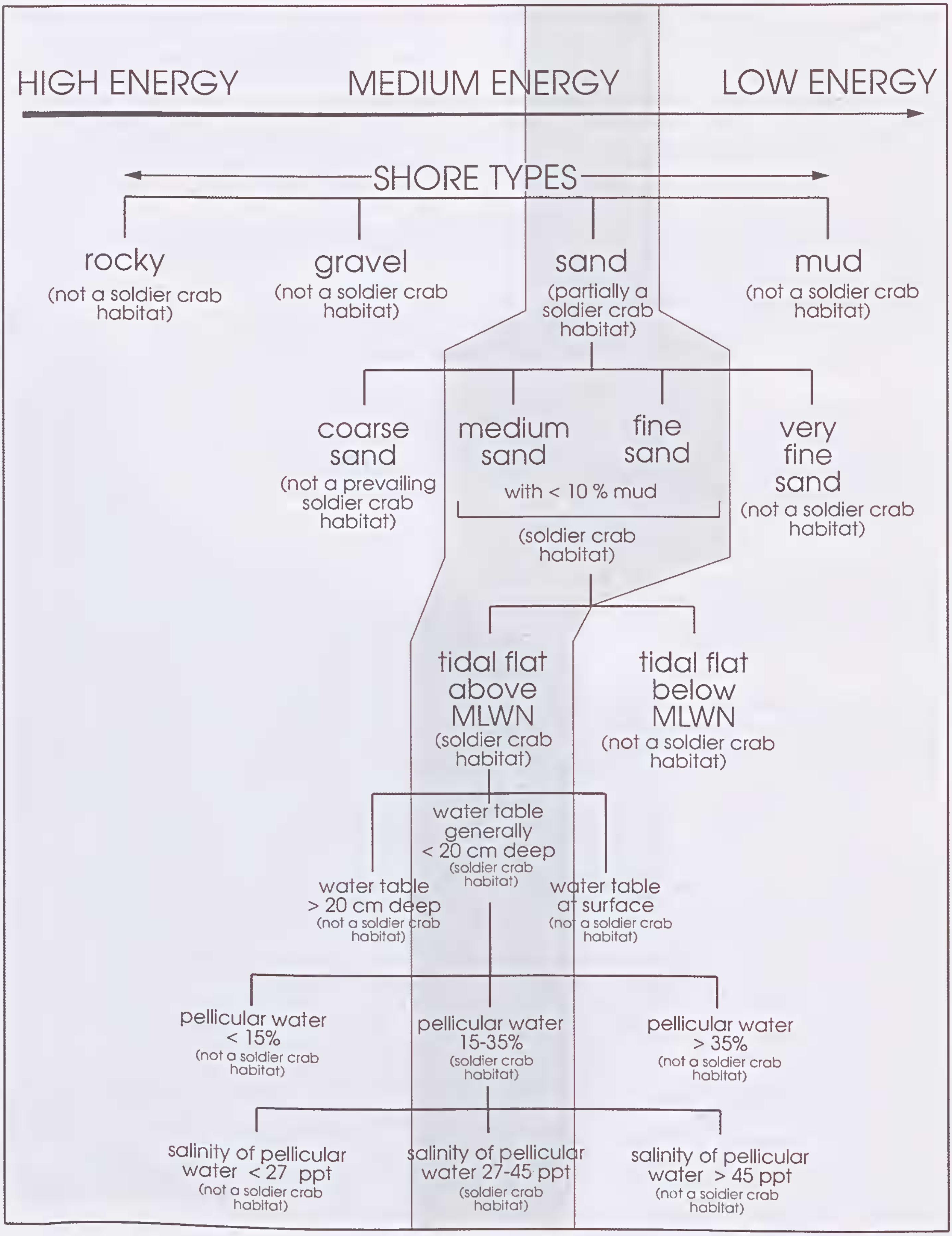


Figure 23. Flow diagram showing the main abiotic features that determine soldier crab occurrence. The diagram is designed so that the range of features (grey tone) that predominantly determine the soldier crab habitats are arranged along a central axis.

Besides sea temperatures, there are other differences between the western and eastern gulfs of Shark Bay, with tidal frequency and tidal range being the most significant in relation to the occurrence of soldier crabs. Tides are semi-diurnal and have a greater tidal range in Hopeless Reach whereas they are diurnal with a lesser tidal range in Freycinet Reach (Burling *et al.* 2003). Every population of soldier crabs along the north-western coast of Western Australia recorded in this study occurred within a semi-diurnal tidal regime, indicating the requirement of low tidal periods for soldier crab activity. The effect of a larger tidal range exposing suitable tidal flat environments thus providing a greater area for soldier crab habitat has been discussed previously. The corollary is that sandy tidal environments that are microtidal and diurnal tides, and particularly those that are low-gradient, may not be ideal soldier crab habitats.

South of Shark Bay, the absence of the soldier crab appears regionally to be determined mainly by coastal types: there is a lack of soldier crab habitats (the extensive rocky shores and cliffs along Edel Land and Zuytdorp Cliffs), and this would appear to be a major factor limiting their occurrence. There also is a lack of suitable habitats between Zuytdorp Cliffs and Kalbarri, in the estuary of the Murchison River, and generally in the islands of the Houtman Abrolhos.

It would appear, therefore, that the Western Australian soldier crab is dominantly a tropical species, with its southern extent delineated by temperature, but rather than temperature having a gradual and sole effect in eliminating the species regionally, the southern biogeographic boundary is sharp because of the lack of suitable habitats in western Shark Bay, and between Shark Bay and the Murchison River estuary, and in the Houtman Abrolhos.

While these northern and southern boundaries to the distribution of the Western Australian soldier crab are relatively sharp, the species is not continuous in its distribution within its biogeographic range. There are large gaps in occurrence because there are no suitable habitats. The high-energy sandy shores of the seafront of the Gascoyne River Delta, the limestone cliffs in the Point Quobba region, and the western shore of the Dampier Peninsula exemplify this (Appendix 1 and Figure 8). The soldier crab habitat is best developed where there are sandy, sheltered embayments, or sandy, sheltered local environments within more open coasts (*i.e.*, sites of small-scale protection). There are various ways in which small-scale protection is developed: in lagoons, in the axis or interior of tidal creeks, in the lee of rocky-knoll outcrops, leeward of rocky barriers, in embayments oriented such that they are sheltered from swell and wind waves, in the lee of low-relief, tidal-flat shoals, leeward of spits, and shoreward of extensive seagrass banks that buffer/dampen wave energy (Figure 8).

Soldier crabs also opportunise sandy high-tidal environments where fresh-water seepages and ebb tide seawater seepages occur. Such seepages dilute the normally hypersaline groundwater and pellicular water that would be present in the high-tidal zone, to replicate low-tidal conditions in terms of salinity and moisture content. This provides another expression of the variability of soldier crab habitat.

A summary of the key factors that eliminate or promote soldier crab occurrence is provided in Figure 23.

The maps of Hearsons Cove and King Bay in Figures 19 and 20 are microcosms of the patterns developed at the subcontinental scale across the Western Australian coast. They illustrate the localised nature of soldier crab habitats. Hearsons Cove, for instance, has a variable suite of tidal habitats, from rocky and bouldery shores, gravelly reflective beaches grading to sandy reflective beaches, low tidal flats underlain by sand or slightly muddy sand, mangrove-vegetated muddy sand, and alluvial sand, most of which are not soldier crab habitats for the reasons of wave energy conditions, unsuitable (rocky) substrate, sand too coarse, groundwater table at low tide too deep or too shallow, groundwater too saline, substrate too muddy, or substrate packed with mangrove pneumatophores. Soldier crab habitats are developed only in local areas where there is a co-incidence of conditions suitable for the species (Figure 23). King Bay presents a similar pattern: amidst rocky shores, muddy sand flats, mangrove-vegetated muddy flats, and wave agitated sand flats, soldier crab habitats are developed where there are locally protected shoals, relatively free of mud, that have become emergent enough to have a groundwater table ~ 10 cm deep. Magnified, these principles of development of the soldier crab habitats in Hearsons Cove and King Bay can be applied to the occurrence of soldier crabs along the Western Australia coast.

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Appendix 1

Regional sampling sites for soldier crabs, with brief description of site.

Some 308 sites were examined along the Western Australian coast between Geraldton and One Arm Point for soldier crab habitats and occurrences of soldier crab populations (Figure 5). Three of the sites recorded by the Western Australian Museum were re-surveyed during this study (*viz.*, Broome Town foreshore, Bay of Rest, and Monkey Mia). Eight sites recorded by the Western Australian Museum were not examined in the field in this study, but are noted in the Table below. To facilitate description of all sites, the coast has been subdivided into twelve tracts, corresponding to natural physiographic and coastal units, and largely corresponding to natural boundaries (Figure 5). These coastal tracts are notated as acronyms. The sampling sites within each tract are numbered sequentially, generally from north to south. Each site within the tract has a unique latitude/ longitude designation. Where a site has a geographic name, this is noted. The presence or absence of soldier crabs at a site is noted. The description of each site relates to the rocky, or sandy, or muddy nature of that tidal part of the shore where soldier crabs might be present, and comments on the nature of the wave energy. For most of the sites selected, there was a focus on settings that were possible or probable soldier crab habitats. However, some of the coastal types selected for field inspection are clearly not soldier crab habitats (*e.g.*, the limestone cliffs shores of the Point Cloates to Point Quobba tract), and many of the high wave energy sandy beaches, but they were examined, for the former in the possibility that pocket beaches supporting soldier crabs may be present (*e.g.*, similar to Black Ledge at Broome), and for the latter in the possibility that seawater seepage from the base of a beach slope may form a local soldier crab habitat. Areas such as Port Hedland (with Nine-mile Creek, Six-mile Creek, the Port Hedland limestone coast, Finucane Island, Salmon Inlet, West Creek, and Salmon Creek), Cape Keraudren, Willie Creek, amongst others, with a multiplicity of sites located in relative latitudinal proximity to each other, illustrate the patchy nature of the shore types and the patchy nature of occurrences of soldier crabs. The information on coastal type and coastal material is presented *also to provide an appreciation of the gaps in soldier crab occurrence along the coast that is due to extensive unavailability of habitat*. For some of the sandy and sheltered locations, where soldier crabs are present, the habitat may not be long-term, *i.e.*, soldier crabs vary in presence/absence from year to year, and if present inter-annually, also markedly vary in abundance from year to year.

A total of 316 sites form part of this study. King Sound (KS) has 31 sites. The Dampier Peninsula coast of the north-western Canning Coast (DP) has 29 sites. The north Canning Coast (between Barn Hill and Cape Bossut = NCC) has 9 sites. The tract of middle to south Canning Coast between Mandora and Pardoo (= SMCC) has 13 sites. The northern Pilbara Coast (between the De Grey River delta and Cossack = NPC) has 25 sites. The Dampier Archipelago to Cape Lambert region (DA-CL) has 27 sites. The southern Pilbara Coast (between the Fortescue River delta and Simpson Island = SPC) has 22 sites. North West Cape (NWC) has 35 sites. The coast between Point Cloates and Point Quobba (PC-PQ) has 10 sites. The Gascoyne River delta regions (GD) has 8 sites. The Shark Bay region (SB) has 72 sites. The coast between Zuytdorp Cliffs and Geraldton (Z-G) has 11 sites. The Houtman Abrolhos (HA) has 24 sites. In the Table below Y = present, N = absent.

This dataset with location of the site as related to Figure 8, the description of coastal site in terms of its wave energy, geomorphology, and substrates, its co-ordinates, and the presence/ absence of soldier crabs is provided as a measure of the variety of coastal types encountered in this study to assess the occurrence of soldier crabs, and as a baseline of the occurrence of *M. occidentalis* along the Western Australian coast that can serve as a comparison for future surveys. In particular, detailed surveys undertaken in the regions of North West Cape, Shark Bay, and Houtman-Abrolhos to define the southern limits of the species, and in the region of the Dampier Peninsula to define the northern limits of the species. provide a measure of the occurrence of the species against the current climate regime and sedimentological setting.

Site #	Location, name, or field notation	Latitude and longitude	Brief description of site	Our Record	WAM Record
KS-01	King Sound tidal flats	17° 0' 20.86" S, 123° 39' 15.87" E	wave agitated and tidally high energy sand flats	N	
KS-02	King Sound tidal flats	17° 1' 24.72" S, 123° 35' 21.56" E	tidally high energy sand and mud flats	N	
KS-03	King Sound tidal flats	17° 2' 1.08" S, 123° 34' 52.32" E	tidally high energy sand and mud flats	N	
KS-04	King Sound tidal flats	17° 5' 16.30" S, 123° 35' 2.78" E	tidally high energy sand and mud flats; rock pavements	N	
KS-05	King Sound tidal flats	17° 11' 12.37" S, 123° 38' 12.26" E	tidally high energy sand shoals	N	
KS-06	King Sound tidal flats	17° 13' 22.39" S, 123° 39' 2.59" E	tidally high energy sand shoals	N	
KS-07	King Sound tidal flats	17° 13' 50.99" S, 123° 36' 47.12" E	tidally high energy sand and mud flats	N	
KS-08	King Sound tidal flats	17° 15' 2.64" S, 123° 32' 11.71" E	tidally high energy sand shoals	N	
KS-09	King Sound tidal flats	17° 16' 44.42" S, 123° 32' 9.13" E	tidally high energy sand shoals	N	
KS-10	King Sound tidal flats	17° 16' 43.60" S, 123° 33' 7.97" E	tidally high energy sand shoals	N	
KS-11	King Sound tidal flats	17° 16' 50.95" S, 123° 36' 38.65" E	tidally high energy sand shoals	N	
KS-12	King Sound tidal flats	17° 17' 25.15" S, 123° 35' 57.73" E	tidally high energy sand shoals	N	
KS-13	King Sound tidal flats	17° 17' 22.63" S, 123° 39' 39.45" E	tidally high energy sand shoals	N	
KS-14	King Sound tidal flats	17° 17' 41.41" S, 123° 32' 44.94" E	tidally high energy sand shoals	N	
KS-15	King Sound tidal flats	17° 17' 56.88" S, 123° 33' 40.38" E	tidally high energy sand shoals	N	
KS-16	King Sound tidal flats	17° 18' 46.40" S, 123° 31' 11.73" E	tidally high energy sand shoals	N	
KS-17	King Sound tidal flats	17° 18' 51.44" S, 123° 32' 47.50" E	tidally high energy sand shoals	N	
KS-18	King Sound tidal flats	17° 18' 56.79" S, 123° 33' 53.76" E	tidally high energy sand shoals	N	
KS-19	King Sound tidal flats	17° 18' 32.89" S, 123° 36' 0.85" E	tidally high energy sand shoals	N	
KS-20	King Sound tidal flats	17° 19' 41.10" S, 123° 32' 12.53" E	tidally high energy sand shoals	N	
KS-21	King Sound tidal flats	17° 19' 44.38" S, 123° 35' 27.04" E	tidally high energy sand shoals	N	
KS-22	King Sound tidal flats	17° 20' 9.60" S, 123° 31' 51.19" E	tidally high energy sand shoals	N	
KS-23	King Sound tidal flats	17° 20' 23.44" S, 123° 36' 1.89" E	tidally high energy sand shoals	N	
KS-24	King Sound tidal flats	17° 20' 21.83" S, 123° 36' 52.36" E	tidally high energy sand flat	N	
KS-25	King Sound tidal flats	17° 20' 58.48" S, 123° 35' 34.73" E	tidally high energy sand shoals	N	
KS-26	King Sound tidal flats	17° 21' 16.34" S, 123° 34' 32.62" E	tidally high energy sand shoals	N	
KS-27	King Sound tidal flats	17° 22' 6.33" S, 123° 33' 49.62" E	tidally high energy sand shoals	N	
KS-28	King Sound tidal flats	17° 23' 19.61" S, 123° 34' 1.57" E	tidally high energy sand shoals	N	
KS-29	King Sound tidal flats	17° 23' 54.83" S, 123° 33' 50.06" E	tidally high energy sand shoals	N	
KS-30	King Sound tidal flats	17° 25' 7.08" S, 123° 32' 52.45" E	tidally high energy sand shoals	N	
KS-31	King Sound tidal flats	17° 25' 58.22" S, 123° 34' 5.10" E	tidally high energy sand shoals	N	
DP-01	One Arm Point	16° 27' 5.61" S, 123° 3' 56.04" E	low tidal sand flats protected from regional swell		Y
DP-02	Cape Leveque North	16° 21' 32.09" S, 123° 2' 1.03" E	high wave energy sand and beach rock coast	N	
DP-03	Cape Leveque South	16° 21' 39.67" S, 123° 1' 43.12" E	high wave energy sand and beach rock coast	N	
DP-04	Lombadina	16° 31' 31.02" S, 122° 52' 19.87" E	low tidal sand flats protected from regional swell	Y	Y
DP-05	North Head to Pender Bay	16° 47' 40.75" S, 122° 33' 44.31" E	high wave energy rocky shore cliff coast	N	
DP-06	North Head	16° 50' 9.12" S, 122° 32' 4.55" E	high wave energy cliff coast	N	
DP-07	Beagle Bay	16° 56' 43.65" S, 122° 30' 52.17" E	low tidal sand flats protected from regional swell	Y	
DP-08	Camp Inlet	16° 56' 56.44" S, 122° 27' 0.07" E	low tidal sand flats protected from regional swell	N	

Site #	Location, name, or field notation	Latitude and longitude	Brief description of site	Our Record	WAM Record
DP-09	west cliff shore Dampier Peninsula	17° 28' 32.18" S, 122° 9' 3.76" E	high wave energy cliff coast	N	
DP-10	Cape Boileau	17° 39' 44.43" S, 122° 11' 1.09" E	high wave energy cliff coast	N	
DP-11	Barred Creek	17° 39' 41.07" S, 122° 11' 18.95" E	low tidal sand shoal in tidal lagoon protected from regional swell by barrier		Y
DP-12	Willie Creek open coast	17° 45' 12.95" S, 122° 11' 42.92" E	high wave energy sand coast to north of Willie Creek	N	
DP-13	Willie Creek area	17° 45' 40.74" S, 122° 12' 16.39" E	low tidal sand shoals in large tidal creek protected from regional swell	Y	
DP-14	Willie Creek area	17° 45' 59.11" S, 122° 12' 21.07" E	low tidal sand floored lagoon protected from regional swell by low sand barrier	Y	
DP-15	Willie Creek area	17° 46' 8.04" S, 122° 12' 13.35" E	low tidal sand-floored lagoon protected from regional swell by low sand barrier	Y	
DP-16	Willie Creek area	17° 46' 43.71" S, 122° 12' 5.52" E	low tidal sand-floored lagoon protected from regional swell by low sand barrier	Y	
DP-17	Willie Creek area	17° 46' 44.77" S, 122° 12' 2.48" E	high wave energy sand coast	N	
DP-18	Willie Creek area	17° 46' 59.22" S, 122° 12' 11.95" E	low tidal sand-floored lagoon protected from regional swell by low sand barrier	Y	
DP-19	Willie Creek area	17° 47' 27.65" S, 122° 12' 6.92" E	high wave energy sand coast	N	
DP-20	Coconut Well tidal lagoon	17° 49' 16.0" S, 122° 12' 45.38" E	high tidal sand-floored lagoon protected from regional swell by low sand barrier (Transect Sites 1 and 2 of this paper)	Y	
DP-21	central Cable Beach	17° 55' 14.98" S, 122° 12' 38.59" E	high wave energy sand coast	N	
DP-22	junction Gantheaume Point with southernmost extremity of Cable Beach	17° 58' 21.27" S, 122° 11' 11.28" E	sand shoals and sand flats leeward (north) of rocky reefs	Y	
DP-23	Entrance Point	18° 0' 29.50" S, 122° 12' 34.93" E	moderate wave energy sand coast with local rocky reef protection (Transect Site 3 of this paper)	Y	
DP-24	north Broome Port	17° 59' 57.75" S, 122° 12' 26.48" E	sand shoals and sand flats leeward (north) of rocky reefs	Y	
DP-25	Broome Town foreshore	17° 58' 02.41" S, 122° 14' 16.00" E	high tidal sand flat leeward of mangroves (Transect Site 4 of this paper)	Y	
DP-26	Black Ledge	17° 58' 9.09" S, 122° 17' 23.37" E	moderate wave energy sand coast with local rocky reef protection	Y	
DP-27	un-named	17° 58' 31.03" S, 122° 21' 3.81" E	high wave energy reflective beach in mid to upper tidal, mud floor between MSL to LAT	N	
DP-28	un-named	17° 59' 9.83" S, 122° 21' 51.85" E	high wave energy reflective beach in mid to upper tidal, mud floor between MSL to LAT	N	
DP-29	Crab Creek	17° 59' 37.78" S, 122° 22' 4.83" E	mud substrates HAT to LAT	N	
NCC-01	Thangoo	18° 09' 38.97" S, 122° 19' 30.50" E	moderate wave energy sand flats amongst and seaward of open mangrove shrubs	Y	
NCC-02	Thangoo south	18° 10' 42.88" S, 122° 16' 54.59" E	moderate wave energy sand flats amongst and seaward of cheniers and open mangrove shrubs	Y	
NCC-03	Cape Villaret -Eco Beach coast	18° 19' 35.96" S, 122° 04' 06.22" E	high wave energy rocky coast and locally sandy beach, with wet low tidal sand flats	N	
NCC-04	Barn Hill coast north	18° 21' 37.15" S, 122° 02' 36.49" E	high wave energy sandy coast, with wet low tidal sand flats	N	
NCC-05	Barn Hill coast central	18° 21' 47.28" S, 122° 02" 23.49" E	high wave energy rocky coast and locally sandy beach, with wet low tidal sand flats	N	
NCC-06	Barn Hill coast south	18° 21' 49.69" S, 122° 02" 11.84" E	high wave energy rocky coast and locally sand flats	N	
NCC-07	Port Smith	18° 30' 41.08" S, 121° 48' 10.25" E	low tidal sand shoal in tidal lagoon protected from regional swell by Holocene limestone barrier	Y	
NCC-08	North Cowan Creek	18° 40' 21.77" S, 121° 45' 54.69" E	low tidal sand flat protected from regional swell by limestone barrier	Y	
NCC-09	Cape Bossut	18° 42' 29.38" S, 121° 37' 30.40" E	high wave energy sand and rock coast	N	
SMCC-01	Mandora North	19° 40' 24.49" S, 120° 51' 18.95" E	low tidal sand shoal in tidal lagoon protected from regional swell by sand barrier	Y	

SMCC-02	Eighty Mile Beach	19° 45' 5.81" S, 120° 40' 20.58" E	low tidal sand flat occurring seaward of a reflective beach	Y
SMCC-03	Shoonta Hill	19° 54' 45.91" S, 120° 10' 54.92" E	high wave energy sand coast	N
SMCC-04	Cape Keraudren area Cootenbrand Creek	19° 58' 20.58" S, 119° 47' 17.55" E	mid-channel creek shoals at ~ MHWN	Y
SMCC-05	Cape Keraudren area northern outer headland	19° 57' 45.54" S, 119° 46' 24.72" E	high wave energy limestone cliff and beach rock coast	N
SMCC-06	Cape Keraudren area outer embayment	19° 5' 41.04" S, 119° 46' 5.10" E	sand flat amongst rocky coast at MSL-MLWN	Y
SMCC-07	Cape Keraudren area mangrove fringe	19° 57' 56.88" S, 119° 46' 13.21" E	sand-floored mangrove fringe between MSL and MHWN	Y
SMCC-08	Cape Keraudren area Mosquito Creek	19° 58' 17.16" S, 119° 46' 33.41" E	sand-floored creek bank at MHWN	Y
SMCC-09	Cape Keraudren area southern outer headland	19° 57' 58.21" S, 119° 45' 06.48" E	high wave energy limestone cliff coast	N
SMCC-10	Red Bluff, NE Pardoo	20° 03' 32.76"" S, 119° 37' 46.02" E	sand tidal flat, and sandy beach amongst limestone rock	Y
SMCC-11	coast NE Pardoo Creek	20° 04' 29.39" S, 119°36' 28.84" E	eroding mud flat in front of low gradient sandy beach	N
SMCC-12	Pardoo Creek mouth	20° 04' 30.70" S, 119° 34' 27.58" E	mud shoals at mouth of tidal creek	N
SMCC-13	Pardoo Creek mid channel shoals	20° 05' 13.73" S, 119° 33' 21.95" E	mid-channel mud shoals in tidal creek	N
NPC-01	De Grey River Delta	19° 58' 30" S, 119° 08' 30" E	low tidal sand shoal in mouth of delta, protected from regional swell	Y
NPC-02	Nine-mile Creek bank	20° 20' 1.03" S, 118° 40' 18.83" E	sand flat amongst mangroves, at ~ MHWN, on bank of tidal creek, protected from regional swell by creek and limestone barrier (Transect Site 5 of this paper)	Y
NPC-03	Nine-mile Creek mid channel	20° 19' 55.68" S, 118° 40' 35.54" E	rippled and megarippled low-tidal sand flats and shoals in mid-channel	N
NPC-04	Nine-mile Creek mouth	20° 19' 31.99" S, 118° 40' 23.47" E	rippled and megarippled low-tidal sand flats and shoals in mid-channel	N
NPC-05	Six-mile Creek shoals	20° 19' 41.03" S, 118° 40' 18.83" E	rippled and megarippled low-tidal sand flats and shoals at mouth of channel	N
NPC-06	Six-mile Creek East, shoals	20°19' 26.24" S, 118° 39' 58.24" E	sand slope and flat, ~ MSL, with seawater discharge from beach, protected from regional swell by creek and limestone barrier	Y
NPC-07	Six-mile Creek East	20° 19' 25.34" S, 118° 39' 53.04" E	sand slope and flat, ~ MSL, with seawater discharge from beach, protected from regional swell by creek and limestone barrier (Transect Site 6 of this paper)	Y
NPC-08	Six-mile Creek West	20° 19' 19.42" S, 118° 39' 50.72" E	sand flat on edge of shoal, ~ MSL, protected from regional swell by creek and limestone barrier (Transect Site 7 of this paper)	Y
NPC-09	Port Hedland coast	20° 18' 44.28" S, 118° 38' 33.2" E	moderate wave energy sand coast	N
NPC-10	Port Hedland coast	20° 18' 26.96" S, 118° 38' 16.66" E	high wave energy sand coast	N
NPC-11	Port Hedland coast	20° 17' 55.76" S, 118° 38' 21.8" E	high wave energy sand coast	N
NPC-12	Port Hedland coast	20° 18' 2.99" S, 118° 37' 42.41" E	high wave energy limestone cliff shore with small pocket beaches	N
NPC-13	Port Hedland coast	20° 18' 19.94" S, 118° 36' 55.34" E	high wave energy limestone cliff shore with small pocket beaches	N
NPC-14	Port Hedland coast	20° 18' 28.35" S, 118° 36' 4.5" E	high wave energy limestone cliff shore with small pocket beaches	N
NPC-15	Port Hedland coast	20° 18' 33.13" S, 118° 34' 55.03" E	high wave energy limestone cliff shore with small pocket beaches	N
NPC-16	Finucane Island 06	20° 17' 52.27" S, 118° 34' 18.93" E	high wave energy limestone cliff	N
NPC-17	Finucane Island 05	20° 17' 49.16" S, 118° 33' 26.85" E	high wave energy limestone cliff	N
NPC-18	Finucane Island 04	20° 18' 1.64" S, 118° 32' 44.83" E	high wave energy limestone cliff	N
NPC-19	Finucane Island 03	20° 18' 12.47" S, 118° 31' 58.78" E	high wave energy limestone cliff	N

Site #	Location, name, or field notation	Latitude and longitude	Brief description of site	Our Record	WAM Record
NPC-20	Finucane Island 02	20° 18' 20.17" S, 118° 31' 35.68" E	high wave energy limestone cliff	N	
NPC-21	Finucane Island 01	20° 18' 25.07" S, 118° 32' 10.58" E	moderate wave energy sand beach	N	
NPC-22	Port Hedland area Downes Island spit	20° 18' 43.25" S, 118° 31' 46.46" E	megarippled and rippled low-tidal sand bar	N	
NPC-23	Port Hedland area Salmon Creek	20° 18' 59.87" S, 118° 32' 32.15" E	megarippled and rippled low-tidal sand bar	N	
NPC-24	Port Hedland area West Creek	20° 18' 37.87" S, 118° 33' 7.01" E	low-tidal mud flats along creek floor	N	
NPC-25	Mundabullungana	20° 22' 20.32" S, 118° 12' 32.04" E	low tidal sand shoal in mouth of tidal creek protected from regional swell delta barriers and by tidal creek		Y
DA-CL-01	East Cossack	20° 40' 30.92" S, 117° 11' 38.08" E	sand flat ~ MHWN on bank of inlet, protected from regional swell by rock ridges and by tidal creek (Transect Site 8 of this paper)	Y	
DA-CL-02	Settlers Beach	20° 40' 3.2" S, 117° 11' 40.24" E	low tidal, low gradient sand flat (dissipative shore) seaward of a reflective beach; also protected from regional swell partly by rock ridges (Transect Site 9 of this paper)	Y	
DA-CL-03	Point Samson	20° 37' 47.46" S, 117° 11' 51.04" E	low tidal, low gradient sand flat (dissipative shore) seaward of a reflective beach; also protected from regional swell partly by rock ridges (Transect Site 10 of this paper)	Y	
DA-CL-04	Mko Bay near Cape Lambert	20° 36' 58.76" S, 117° 11' 4.29" E	low tidal sand shoal in tidal lagoon protected from regional swell by sand barrier and partly by rock ridges	Y	
DA-CL-05	Cleaverville	20° 39' 45.81" S, 116° 59' 1.38" E	high wave energy rocky shore	N	
DA-CL-06	Nickol Bay coast	20° 42' 40.51" S, 116° 55' 26.15" E	low tidal sand shoals, mouth of the Nickol River	Y	
DA-CL-07	Nickol Bay coast	20° 43' 14.81" S, 116° 53' 24.6" E	limestone pavement shore with mud veneer	N	
DA-CL-08	Nickol Bay coast	20° 43' 16.63" S, 116° 51' 56.69" E	limestone pavement shore with mud veneer	N	
DA-CL-09	Hearsons Cove	20° 37' 42.14" S, 116° 47' 51.41" E	reflective beach and low gradient dissipative shore, with low tidal shoal complex; also high tidal alluvial fan (Transect Sites 11, 12, 13 of this paper)	Y	
DA-CL-10	Searipple Passage	20° 31' 13.33" S, 116° 50' 57.45" E	low tidal limestone pavement and mid tidal mud slope	N	
DA-CL-11	Searipple Passage	20° 31' 18.8" S, 116° 49' 54.69" E	low tidal limestone pavement and mid tidal mangrove-vegetated mud slope	N	
DA-CL-12	Legendre Island	20° 22' 30.63" S, 116° 50' 42.33" E	limestone rocky shore and high energy sandy beach	N	
DA-CL-13	Malus Island north	20° 13' 07.88" S, 116° 40' 56.53" E	high energy sandy beach	N	
DA-CL-14	Malus Island central	20° 30' 30.90" S, 116° 40' 16.84" E	high energy sandy beach	N	
DA-CL-15	Malus Island west	20° 31' 15.40" S, 116° 39' 30.63" E	high energy sandy beach	N	
DA-CL-16	Noname Bay	20° 36' 07.53" S, 116° 45' 45.81" E	moderate wave energy sand flats	N	
DA-CL-17	Tozer Island	20° 27' 22.31" S, 116° 50' 34.46" E	low tidal sand flat in embayment		Y
DA-CL-18	Angel Island	20° 28' 11.55" S, 116° 48' 24.13" E	moderate wave energy low tidal sand flat and limestone	N	
DA-CL-19	Angel Island	20° 30' 7.41" S, 116° 47' 37.52" E	moderate wave energy low tidal sand flat and limestone	N	
DA-CL-20	Conzinc Bay	20° 32' 22.66" S, 116° 48' 50.52" E	moderate wave energy sand flats and tidal rock/gravel pavement	N	
DA-CL-21	Withnell Bay	20° 34' 17.87" S, 116° 47' 46.68" E	low wave energy low tidal sand flat (Transect Site 14 of this paper)	Y	
DA-CL-22	King Bay	20° 38' 10.38" S, 116° 45' 28.87" E	low wave energy low tidal sand shoals, sand bar, and tidal creel shoals (Transect Sites 15, 16 17, 18 of this paper)	Y	
DA-CL-23	Lewis Island	20° 36' 11.13" S, 116° 38' 33.62" E	moderate wave energy low tidal sand flat	N	
DA-CL-24	West Lewis Island	20° 33' 53.52" S, 116° 38' 17.54" E	low tidal sand flat sheltered from regional swell		Y
DA-CL-25	Enderby Island	20° 35' 49.08" S, 116° 31' 23.13" E	moderate to high wave energy beach	N	

DA-CL-26	East Maitland River Delta	20° 43' 35.97" S, 116° 36' 9.45" E	low tidal limestone pavement	N	
DA-CL-27	Maitland River Delta	20° 45' 6.43" S, 116° 31' 55.11" E	dissipative sand flats at delta front, partly protected by the Archipelago islands, and tidal lagoon leeward of sand barrier	Y	
SPC-01	Fortescue River delta	21° 0' 2.4" S, 116° 6' 41.3" E	limestone pavement	N	
SPC-02	Fortescue River delta	20° 59' 58.72" S, 116° 6' 22.15" E	limestone pavement and sand flats	N	
SPC-03	Fortescue River delta	21° 1' 21.19" S, 116° 2' 18.66" E	sand flats with mangroves	N	
SPC-04	Fortescue River delta	21° 11' 10.34" S, 115° 50' 50.83" E	sand flats	N	
SPC-05	Robe River delta limestone barrier	21° 23' 51.35" S, 115° 33' 59.87" E	cliff and pavement cut into limestone	N	
SPC-06	Mangrove Islands	21° 31' 22.82" S, 115° 27' 5.56" E	mid-tidal sand cuspate form sheltered from regional swell by limestone island	Y	
SPC-07	North Onslow coast	21° 35' 34.9" S, 115° 17' 32.16" E	high wave energy shore of limestone pavement and sandy beach	N	
SPC-08	Yammerdery Island	21° 34' 36.75" S, 115° 13' 32.16" E	cliff and pavement cut into limestone	N	
SPC-09	Onslow coast	21° 38' 18.07" S, 115° 8' 32.39" E	high wave energy beach	N	
SPC-10	Onslow coast	21° 38' 31.93" S, 115° 8' 33.95" E	high wave energy beach	N	
SPC-11	Onslow coast	21° 38' 32.79" S, 115° 7' 37.98" E	high wave energy beach	N	
SPC-12	Onslow coast	21° 38' 6.7" S, 115° 6' 48.35" E	high wave energy beach and low tidal limestone pavement	N	
SPC-13	Onslow coast	21° 38' 14.01" S, 115° 6' 2.91" E	high wave energy beach	N	
SPC-14	Onslow coast	21° 39' 21.36" S, 115° 4' 53.52" E	high wave energy beach	N	
SPC-15	Onslow coast	21° 41' 23.02" S, 115° 3' 32.07" E	high wave energy beach	N	
SPC-16	Onslow coast	21° 40' 45.15" S, 115° 2' 57.78" E	open coast is high wave energy beach; soldier crab habitat located in axis of tidal creek sheltered from swell and wind waves (Transect Site 19 of this paper)	Y	
SPC-17	Ashburton River delta mouth	21° 40' 37.57" S, 114° 59' 29.52" E	high wave energy beach on open delta shore	N	
SPC-18	Ashburton River delta mouth	21° 41' 25.34" S, 114° 55' 23.07" E	high wave energy beach on open delta shore	N	
SPC-19	Burnside Island	22° 0' 48.95" S, 114° 30' 03.85" E	high wave energy beach and low tidal limestone pavement	N	
SPC-20	Hope Island	22° 6' 7.58" S, 114° 30' 40.38" E	mud on limestone pavement	N	
SPC-21	Simpson Island NE	22° 7' 18.48" S, 114° 29' 16.93" E	limestone shore: cliff and pavement	Y	
SPC-22	Simpson Island SE	22° 8' 6.83" S, 114° 29' 21.79" E	sheltered low-tidal sand flat leeward of spit		Y
NWC-01	Bay of Rest	22° 31' 40.22" S, 114° 09' 23.11" E	low-tidal sand flat within sheltered embayment	Y	
NWC-02	Little Bay of Rest	22° 24' 02.05" S, 114° 08' 10.52" E	low-tidal sand flat within sheltered embayment	Y	
NWC-03	Bay of Rest (WAM collection site)	22° 23' 57.84" S, 114° 8' 11.89" E	low-tidal sand flat within sheltered embayment		Y
NWC-04	Little Bay of Rest	22° 18' 38.24" S, 114° 7' 43.84" E	low-tidal sand flat within sheltered embayment	Y	
NWC-05	Learmonth Jetty, North West Cape	22° 12' 40.78" S, 114° 05' 58.92" E	high wave energy beach	N	
NWC-06	North West Cape	22° 12' 16.06" S, 114° 05' 34.00" E	high wave energy beach	N	
NWC-07	North West Cape	22° 09' 47.75" S, 114° 04' 58.50" E	high wave energy beach with limestone pavement, and low spring tide shoals/depressions	N	
NWC-08	North West Cape	22° 08' 37.74" S, 114° 05' 04.69" E	high wave energy beach with limestone pavement, and low spring tide shoals/depressions	N	
NWC-09	North West Cape	22° 08' 24.56" S, 114° 05' 06.40" E	high wave energy beach with limestone pavement, and low spring tide shoals/depressions	N	

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NWC-10	North West Cape	22° 07' 36.05" S, 114° 05' 17.34" E	high wave energy beach with limestone pavement, and low spring tide shoals/depressions	N	
NWC-11	North West Cape	22° 06' 44.69" S, 114° 05' 38.30" E	high wave energy beach with limestone pavement, and low spring tide shoals/depressions	N	
NWC-12	Pebble Beach, North West Cape	22° 02' 28.56" S, 114° 06' 55.72" E	high wave energy beach with sand and pebbles	N	
NWC-13	Exmouth Town Beach, North West Cape	21° 57' 32.61" S, 114° 08' 22.06" E	high wave energy beach with low spring tide shoals/depressions	N	
NWC-14	North of Exmouth town, North West Cape	21° 53' 25.96" S, 114° 8' 45.74" E	high wave energy beach	N	
NWC-15	Bundegi Sanctuary middle, North West Cape	21° 52' 15.78" S, 114° 8' 54.16" E	high wave energy beach	N	
NWC-16	Bundegi Sanctuary north, North West Cape	21° 51' 17.75" S, 114° 9' 22.55" E	high wave energy beach	N	
NWC-17	Coral View, North West Cape	21° 50' 13.78" S, 114° 10' 12.21" E	high wave energy beach	N	
NWC-18	Navy Pier, North West Cape	21° 48' 51.33" S, 114° 11' 27.48" E	high wave energy beach	N	
NWC-19	Mildura Wreck, North West Cape	21° 47' 7.82" S, 114° 9' 54.15" E	high wave energy limestone cliff shore	N	
NWC-20	Vlamingh Head Lighthouse, North West Cape	21° 48' 9.77" S, 114° 6' 31.93" E	high wave energy beach	N	
NWC-21	Hunter's Beach, North West Cape	21° 48' 19.84" S, 114° 6' 4.76" E	high wave energy beach	N	
NWC-22	Bauden, North West Cape	21° 50' 47.20" S, 114° 2' 17.42" E	high wave energy beach	N	
NWC-23	False Is Pt south, North West Cape	21° 51' 24.90" S, 114° 1' 13.57" E	high wave energy beach	N	
NWC-24	Tantabiddi , North West Cape	21° 54' 44.07" S, 113° 58' 42.14" E	high wave energy beach	N	
NWC-25	Mangrove Bay north North West Cape	21° 57' 51.71" S, 113° 56' 33.42" E	high wave energy beach and limestone	N	
NWC-26	Mangrove Bay; North West Cape	21° 58' 17.17" S, 113° 56' 24.89" E	mangrove and sandy beach fringed embayment protected from regional swell and wind waves by a barrier spit (Transect Site 20 of this paper)	Y	
NWC-27	T-bone Bay' North West Cape	22° 01' 27.07" S, 113° 55' 11.35" E	high wave energy beach	N	
NWC-28	Trealla Beach, North West Cape	22° 02' 59.49" S, 113° 54' 26.98" E	high wave energy beach	N	
NWC-29	Tulki Beach, North West Cape	22° 04' 29.57" S, 113° 53' 46.92" E	high wave energy beach	N	
NWC-30	North Mandu, North West Cape	22° 08' 32.52" S, 113° 52' 17.15" E	high wave energy beach	N	
NWC-31	South Mandu' North West Cape	22° 08' 42.90" S, 113° 52' 12.93" E	high wave energy beach	N	

NWC-32	North West Cape	22° 10' 2.91" S, 113° 51' 43.30" E	high wave energy beach	N
NWC-33	Pilgrammunna, North West Cape	22° 11' 35.28" S, 113° 51' 21.58" E	high wave energy beach	N
NWC-34	Sandy Bay, North West Cape	22° 13' 50.89" S, 113° 50' 33.31" E	high wave energy beach	N
NWC-35	Yardie Creek, North West Cape	22° 19' 25.71" S, 113° 48' 45.51" E	high wave energy shoal barring a marine flooded sand-fringed ravine	N
PC-PQ-01	Point Cloates – Point Quobba coast	22° 40' 8.05" S, 113° 41' 10.68" E	high wave energy beach	N
PC-PQ-02	Point Cloates – Point Quobba coast	23° 08' 12.5" S, 113° 46' 0.06" E	high wave energy beach	N
PC-PQ-03	Point Cloates – Point Quobba coast	24° 00' 3.17" S, 113° 27' 40.39" E	high wave energy beach	N
PC-PQ-04	Point Cloates – Point Quobba coast	24° 4' 58.85" S, 113° 25' 38.64" E	high wave energy cliff shore	N
PC-PQ-05	Point Cloates – Point Quobba coast	24° 7' 5.85" S, 113° 25' 57.72" E	high wave energy cliff shore	N
PC-PQ-06	Point Cloates – Point Quobba coast	24° 13' 33.79" S, 113° 23' 39.57" E	high wave energy cliff shore	N
PC-PQ-07	Point Cloates – Point Quobba coast	24° 23' 50.54" S, 113° 24' 12.74" E	high wave energy cliff shore	N
PC-PQ-08	Point Cloates – Point Quobba coast	24° 26' 34.83" S, 113° 24' 16.46" E	high wave energy cliff shore	N
PC-PQ-09	Point Cloates – Point Quobba coast	24° 28' 40.89" S, 113° 24' 24.64" E	high wave energy cliff shore	N
PC-PQ-10	Point Cloates – Point Quobba coast	24° 29' 12.50" S, 113° 24' 33.40" E	high wave energy cliff shore	N
GD-01	Gascoyne delta coast	24° 39' 57.65" S, 113° 33' 33.31" E	high wave energy sand shore	N
GD-02	Gascoyne delta coast	24° 43' 58.16" S, 113° 36' 51.12" E	high wave energy sand shore	N
GD-03	Gascoyne delta coast	24° 47' 55.76" S, 113° 37' 58.23" E	high wave energy sand shore	N
GD-04	Gascoyne delta coast	24° 51' 43.88" S, 113° 37' 43.00" E	tidal creek within strand plain protected from regional swell and wind waves (Transect Site 21 of this paper)	Y
GD-05	Gascoyne delta coast	24° 52' 36.60" S, 113° 37' 34.46" E	tidal lagoon within strand plain protected from regional swell and wind waves (Transect Site 22 of this paper)	Y
GD-06	Gascoyne delta coast	24° 52' 38.74" S, 113° 37' 30.72" E	tidal creek within strand plain protected from regional swell and wind waves (Transect Site 23 of this paper)	Y
GD-07	The Fascine, Gascoyne delta coast	24° 53' 3.96" S, 113° 39' 10.96" E	sand shoals within main channel of the Gascoyne River; protected from regional swell and wind waves by location in channel	Y
GD-08	Mangrove Point, Gascoyne Delta coast	24° 54' 19.45" S, 113° 39' 15.56" E	moderate to low wave energy sand flats amongst and seaward of open mangrove shrubs (Transect Site 24 of this paper)	Y
SB01	Gascoyne Flats, north-eastern extremity of Shark Bay	24° 54' 44.71" S, 113° 40' 17.88" E	moderate wave energy sand flats shoreward of a seagrass-vegetated platform	Y
SB02	Uendoo Creek, north-eastern Shark Bay	25° 03' 13.50" S, 113° 40' 49.68" E	moderate wave energy muddy sand flats in front of mangroves, and shoreward of a seagrass-vegetated platform	N

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SB03	Bush Bay, north-eastern Shark Bay	25° 07' 52.32" S, 113° 45' 17.10" E	moderate to high wave energy sand flats and sand ridges, and sand flats adjoining mangroves, shoreward of a seagrass-vegetated platform	N	
SB04	New Beach, north-eastern Shark Bay	25° 08' 50.58" S, 113° 46' 49.26" E	moderate to high wave energy sand flats and sand ridges, and sand flats adjoining mangroves, shoreward of a seagrass-vegetated platform	N	
SB05	north-eastern Shark Bay	25° 11' 05.08" S, 113° 49' 29.61" E	moderate to high wave energy sand flats and sand ridges, and sand flats adjoining mangroves, shoreward of a seagrass-vegetated platform	N	
SB06	north-eastern Shark Bay	25° 11' 51.72" S, 113° 49' 44.52" E	moderate to high wave energy sand flats and sand ridges, and sand flats adjoining mangroves, shoreward of a seagrass-vegetated platform	N	
SB07	north-eastern Shark Bay	25° 15' 42.41" S, 113° 50' 55.64" E	moderate to high wave energy sand flats and algal mat covered sand flats seaward of and adjoining mangroves, leeward of a north-oriented spit, shoreward of a seagrass-vegetated platform	N	
SB08	north-eastern Shark Bay	25° 17' 52.64" S, 113° 52' 02.68" E	moderate to high wave energy sand flats and algal mat covered sand flats seaward of, and adjoining mangroves, leeward of a north-oriented spit, shoreward of a seagrass-vegetated platform	N	
SB09	north-eastern Shark Bay	25° 20' 34.14" S, 113° 53' 32.58" E	moderate to high wave energy sand flats and algal mat covered sand flats seaward of and adjoining mangroves, leeward of a north-oriented spit, shoreward of a seagrass-vegetated platform	N	
SB10	north-eastern Shark Bay	25° 23' 16.81" S, 113° 54' 21.85" E	moderate wave energy sand flats and algal mat covered sand flats seaward of and adjoining mangroves, leeward of a north-oriented spit, shoreward of a seagrass-vegetated platform	N	
SB-11	eastern Shark Bay coast	25° 49' 21.36" S, 114° 11' 34.06" E	sand flats at front of wave-dominated Wooramel River delta	N	
SB-12	Gladstone Embayment, mid-eastern Shark Bay coast	25° 56' 58.66" S, 113° 14' 53.59" E	algal mat covered tidal flat	N	
SB-13	barrier to Gladstone Embayment, mid-eastern Shark Bay coast	25° 58' 24.18" S, 114° 13' 16.25" E	moderate wave energy beaches and cheniers, with adjoining algal mat covered tidal flat	N	
SB-14	Hutchison Embayment, south-eastern Hamelin Pool, Shark Bay coast	26° 09' 17.82" S, 114° 12' 33.87" E	stromatolite tidal shore and shell grit	N	
SB-15	Goat Point, south-eastern Hamelin Pool, Shark Bay coast	26° 15' 48.03" S, 114° 13' 09.19" E	stromatolite tidal shore, moderate wave energy beaches, and shell grit	N	
SB-16	Nilemah Embayment, southern Hamelin Pool, Shark Bay coast	26° 27' 00.91" S, 114° 05' 19.18" E	moderate wave energy beach, shell grit spits, and algal mat covered tidal flat	N	
SB-17	south-western Hamelin Pool, Shark Bay coast	26° 24' 01.42" S, 114° 02' 10.48" E	moderate wave energy beach with shell grit and stromatolite tidal shore	N	
SB-18	western Hamelin Pool, Shark Bay coast	26° 12' 54.65" S, 113° 56' 18.76" E	moderate wave energy beach with shell grit and stromatolite tidal shore	N	
SB-19	Shell Beach, southern L'Haridon Bight, Shark Bay coast	26° 12' 48.88" S, 113° 46' 04.93" E	moderate wave energy beach with shell grit, and algal mat on tidal flat	N	
SB-20	west of Shell Beach, southern L'Haridon Bight, Shark Bay coast	26° 12' 52.05" S, 113° 46' 27.55" E	moderate wave energy beach with shell grit, and algal mat on tidal flat	N	

SB-21	western L'Haridon Bight, Shark Bay coast	26° 05' 36.84" S, 113° 42' 10.40" E	algal mats, breccia pavements, shell pavements, shell grit spits	N	
SB-22	north Faure Island, Shark Bay coast	25° 48' 01.64" S, 113° 52' 40.86" E	sand flat, shell pavements, mussel beds, muddy sand mangrove shore, beach ridges	N	
SB-23	northwest Faure Island, Shark Bay coast	25° 48' 20.43" S, 113° 51' 56.79" E	sand flat, shell pavements, mussel beds, muddy sand mangrove shore, spits with muddy sediment to leeward	N	
SB-24	west Faure Island, Shark Bay coast	25° 50' 35.76" S, 113° 51' 11.47" E	spit barrier shore with sand flats and shell pavement mangrove, samphire and algal mats to leeward, sand flats and shell pavement to seaward	N	
SB-25	southwest Faure Island, Shark Bay coast	25° 51' 41.63" S, 113° 51' 19.70" E	spit barrier shore with sand flats and shell pavement mangrove, samphire and a lgal mats to leeward, sand flats and shell pavement to seaward	N	
SB-26	Dubaut Point, west shore of Faure Sill, Shark Bay coast	25° 56' 18.52" S, 113° 44' 12.06" E	algal mats, shell pavements, sand spits	N	
SB-27	west shore of Faure Sill, Shark Bay coast	25° 52' 8.59" S, 113° 44' 36.37" E	algal mats, shell pavements, sand spits	N	
SB-28	Dubaut Creek mouth, west shore of Faure Sill, Shark Bay coast	25° 51' 42.19" S, 113° 43' 37.13" E	sand beachridges, mangroves on muddy sand, muddy sand tidal flats, and water-logged sand flats	N	
SB-29	sand flats north of Dubaut Creek, Shark Bay coast	25° 51' 13.11" S, 113° 43' 16.68" E	low tidal sand flats are soldier crab depauperate; soldier crab habitat on low shoals amongst mangrove copses	Y	
SB-30	sand flats south of Monkey Mia, Shark Bay coast	25° 49' 45.00" S, 113° 43' 20.38" E	low tidal sand flats in a shoal and depression complex on a moderate energy beach	Y	
SB-31	spit south of Monkey Mia, Shark Bay coast	25° 48' 0.17" S, 113° 43' 21.94" E	low tidal shell pavement leeward of sandy spit	N	
SB-32	Monkey Mia, Shark Bay coast	25° 47' 42.32" S, 113° 43' 22.62" E	low tidal sand flat leeward of a shoreline spit, and subregionally protected by a large seagrass-vegetated submarine spit (Transect Site 25 of this paper)	Y	Y
SB-33	Red Cliff, Shark Bay coast	25° 47' 23.12" S, 113° 41' 36.62" E	low tidal sand flats in a shoal and depression complex on a moderate energy beach	Y	
SB-34	Cape Rose, Shark Bay coast	25° 44' 02.70" S, 113° 37' 47.04" E	low tidal sand flats in a shoal and depression complex on a moderate energy beach	Y	
SB-35	eastern Guichenault Point, Shark Bay coast	25° 37' 3.96" S, 113° 34' 56.40" E	sand flats and shell pavements comprising a north-trending spit, moderate wave energy	N	
SB-36	western Guichenault Point, Shark Bay coast	25° 37' 6.72" S, 113° 34' 44.64" E	sand flats and shell pavements on tidal flats between two north-trending spits, moderate wave energy	N	
SB-37	Herald Bight, inshore tidal flat, Shark Bay coast	25° 37' 51.03" S, 113° 33' 1.58" E	sand flats and shell pavements on tidal flats seaward of a beachridge, moderate wave energy	N	
SB-38	Skipjack Rocks (site 1), Peron Peninsula, Shark Bay coast	25° 30' 54.36" S, 113° 31' 2.40" E	sand flats and shelly sand seaward of a beach, moderate wave energy	N	
SB-39	Skipjack Rocks (site 2), Peron Peninsula, Shark Bay coast	25° 30' 49.41" S, 113° 30' 53.88" E	sand flats and shelly sand seaward of a beach, moderate wave energy	N	
SB-40	Point Leuseur, north-western Peron Peninsula, Shark Bay coast	25° 43' 5.28" S, 113° 24' 59.46" E	sand flats, shelly sand, algal mats, and mangrove flats leeward and seaward of a sandy spit complex; high wave energy	N	

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SB-41	Big Lagoon complex (site 1), north-western Peron Peninsula, Shark Bay coast	25° 47' 45.00" S, 113° 27' 58.02" E	sheltered sand flats, shelly sand, water saturated sand flats, algal mats, and mangrove flats leeward of a sandy spit complex;	N	
SB-42	Big Lagoon complex (site 2), north-western Peron Peninsula, Shark Bay coast	25° 48' 20.26" S, 113° 27' 49.13" E	sand flats, shelly sand seaward of a sandy spit complex; high wave energy	N	
SB-43	Little Lagoon complex: open coast at mouth of creek, Shark Bay coast	25° 54' 12.01" S, 113° 31' 23.47" E	low tidal sand flats and shell pavements, high energy	N	
SB-44	Little Lagoon complex: barred ebb delta shoals at mouth of creek, Shark Bay coast	25° 54' 6.49" S, 113° 31' 26.05" E	low tidal sand flats and deep water channel	N	
SB-45	Little Lagoon complex: mid channel shoals interior of creek, Shark Bay coast	25° 54' 20.15" S, 113° 31' 43.16" E	sheltered low tidal sand and muddy sand flats and algal mats and fringing mangrove	N	
SB-46	Little Lagoon complex: flood delta shoals at east of creek, Shark Bay coast	25° 54' 7.94" S, 113° 31' 52.98" E	sheltered low tidal shell pavement and sand flats and algal mats and fringing mangrove	N	
SB-47	Shark Bay coast south of Little Lagoon	25° 54' 34.98" S, 113° 31' 15.00" E	spit and sheltered lagoon complex, with sand, shell pavements	N	
SB-48	Lagoon Point, Shark Bay coast	25° 55' 7.02" S, 113° 30' 58.98" E	spit and lagoon complex, with sand, shell pavements, gravel pavement	N	
SB-49	Shark Bay coast between Lagoon Point and Denham	25° 55' 20.24" S, 113° 31' 18.05" E	moderate wave energy beach and sand flats	N	
SB-50	Denham foreshore, Shark Bay coast	25° 55' 39.37" S, 113° 31' 50.93" E	moderate wave energy beach and sand flats	N	
SB-51	Eagle Bluff, Shark Bay coast	26° 05' 34.08" S, 113° 34' 45.1" E	moderate wave energy beach	N	
SB-52	spit and lagoon complex within cove, Shark Bay coast	26° 06' 22.02" S, 113° 37' 10.98" E	algal mats, muddy sand and low-tidal water saturated sand	N	
SB-53	spit and lagoon complex, Shark Bay coast	26° 11' 37.02" S, 113° 41' 10.98" E	algal mats and shell pavements	N	
SB-54	Goulet Bluff spit and lagoon complex, Shark Bay coast	26° 12' 51.00" S, 113° 41' 25.02" E	algal mats and shell pavements	N	
SB-55	Goulet Bluff - Nanga tract site 1, Shark Bay coast	26° 13' 26.76" S, 113° 42' 36.39" E	moderate wave energy sandy and shelly beach and pocket beach between rocky coast	N	
SB-56	Goulet Bluff - Nanga tract site 2, Shark Bay	26° 13' 45.07" S, 113° 44' 01.39" E	moderate wave energy sandy and shelly beach adjoining a rocky shore	N	

	coast			
SB-57	Goulet Bluff - Nanga tract site 3, Shark Bay coast	26° 14' 15.40" S, 113° 45' 59.29" E	moderate wave energy sandy and shelly beach and beachridge and pocket beach between rocky coast	N
SB-58	Goulet Bluff - Nanga tract site 4, Shark Bay coast	26° 14' 45.40" S, 113° 47' 15.67" E	moderate wave energy sandy and shelly beach and pocket beach between rocky coast	N
SB-59	Nanga Station coast, Shark Bay coast	26° 15' 21.76" S, 113° 48' 10.60" E	moderate wave energy sandy and shelly beach adjoining a rocky shore	N
SB-60	Garden Point, Shark Bay coast	26° 23' 59.41" S, 113° 51' 57.45" E	moderate wave energy sand and shell spit shore, with algal mats to leeward	N
SB-61	southern Disappointment Loop, Shark Bay coast	26° 39' 46.29" S, 113° 40' 4.03" E	stromatolite shore and shell grit	N
SB-62	southern Depuch Loop, Shark Bay coast	26° 34' 19.89" S, 113° 33' 39.82" E	limestone rocky shore and sandy beaches	N
SB-63	north-western Depuch Loop, Shark Bay coast	26° 27' 46.56" S, 113° 33' 31.92" E	limestone rocky shore and sandy beaches	N
SB-64	east shore Carrarang Peninsula, Shark Bay coast	26° 19' 42.07" S, 113° 32' 42.12" E	moderate wave energy beach	N
SB-65	north Carrarang Peninsula site 1, Shark Bay coast	26° 17' 34.20" S, 113° 32' 23.21" E	sand flats and shell pavements comprising north-trending spit, and the tidal flats leeward and seaward of the spit	N
SB-66	north Carrarang Peninsula site 2, Shark Bay coast	26° 16' 32.74" S, 113° 30' 38.75" E	sand flats and shell pavements comprising north-trending spit, and the tidal flats leeward and seaward of the spit	N
SB-67	north Carrarang Peninsula site 3, Shark Bay coast	26° 18' 23.85" S, 113° 29' 44.45" E	sand flats and shell pavements comprising north-trending spit; algal mats and muddy sand to leeward of the spit	N
SB-68	north Carrarang Peninsula site 4, Shark Bay coast	26° 19' 16.69" S, 113° 30' 32.19" E	moderate energy sand flats and beach protected by a north-trending limestone peninsula	N
SB-69	southern shore, Brown Inlet, Shark Bay coast	26° 29' 0.63" S, 113° 29' 10.83" E	shelly beach	N
SB-70	Ant Island, Shark Bay coast	26° 09' 47.64" S, 113° 26' 37.27" E	limestone rocky shore, limestone pavement, sandy beaches	N
SB-71	spit shore north-eastern Useless Loop, Shark Bay coast	26° 08' 13.98" S, 113° 25' 43.02" E	limestone rocky shore, limestone pavement, sandy beaches, shelly sand	N
SB-72	Steep Point	26° 08' 54.66" S, 113° 09' 39.46" E	high wave energy cliff	N
ZC-G-01	Zuytdorp Cliffs	26° 50' 20.96" S, 113° 42' 53.20" E	high wave energy cliff	N
ZC-G-02	coast north of Kalbarri	27° 15' 55.66" S, 113° 59' 03.78" E	high wave energy beach	N
ZC-G-03	coast north of Kalbarri	27° 29' 31.48" S, 114° 05' 56.90" E	high wave energy beach	N
ZC-G-04	coast north of Kalbarri	27° 32' 41.78" S, 114° 06' 53.19" E	high wave energy beach	N
ZC-G-05	north of Kalbarri 1	27° 36' 32.49" S, 114° 08' 21.72" E	high wave energy beach	N
ZC-G-06	Murchison River estuary, Kalbarri	27° 42' 25.19" S, 114° 09' 38.67" E	moderate wave energy shoals at estuary entrance (freshwater influenced)	N

Site #	Location, name, or field notation	Latitude and longitude	Brief description of site	Our Record	WAM Record
ZC-G-07	Murchison River estuary, Kalbarri	27° 41' 58.91" S, 114° 09' 55.37" E	low wave energy shoals within estuary (freshwater influenced)	N	
ZC-G-08	Murchison River estuary, Kalbarri	27° 41' 32.45" S, 114° 10' 14.58" E	low wave energy shoals within estuary (freshwater influenced)	N	
ZC-G-09	Murchison River estuary, Kalbarri	27° 41' 9.44" S, 114° 10' 28.58" E	low wave energy shoals within estuary (freshwater influenced)	N	
ZC-G-10	Oakajee coast	28° 39' 33.68" S, 114° 36' 40.40" E	high wave energy beach	N	
ZC-G-11	Geraldton coast	28° 46' 47.86" S, 114° 34' 37.17" E	high wave energy beach	N	
HA-01	Houtman Abrolhos	28° 17' 34.44" S, 113° 35' 53.96" S	high wave energy beach	N	
HA-02	Houtman Abrolhos	28° 17' 48.59" S, 113° 36' 1.92" E	high wave energy beach	N	
HA-03	Houtman Abrolhos	28° 28' 30.77" S, 113° 41' 48.71" E	tidal creel shoal underlain by coarse -/ very coarse sand on limestone pavement or gravel	N	
HA-04	Houtman Abrolhos	28° 28' 23.88" S, 113° 41' 49.06" E	sand protecting small cove; spit is very coarse sand; cove is underlain by veneer of sand and mud on limestone pavement	N	
HA-05	Houtman Abrolhos	28° 29' 43.65" S, 113° 46' 4.92" E	sand with worm tubes, flanked by coarse coral gravel	N	
HA-06	Houtman Abrolhos	28° 40' 5.44" S, 113° 49' 41.94" E	coarse and very sand and medium sand, with some mud layers underling beach	N	
HA-07	Houtman Abrolhos	28° 43' 24.70" S, 113° 50' 07.99" E	beach with coarse sand and gravel, veneer on limestone pavement	N	
HA-08	Houtman Abrolhos	28° 43' 28.72" S, 113° 50' 04.03" E	sandy beach with veneer on limestone pavement of coarse and medium sand (with worm tubes)	N	
HA-09	Houtman Abrolhos	28° 44' 41.75" S, 113° 48' 41.79" E	high wave energy coral gravel shore and ridges; coarse – medium sand over limestone pavement	N	
HA-10	Houtman Abrolhos	28° 40' 6.03" S, 113° 49' 43.52" E	high wave energy coral gravel shore and ridges; coarse – medium sand over limestone pavement	N	
HA-11	Houtman Abrolhos	28° 40' 11.90" S, 113° 49' 46.98" E	shore parallel ribbon of sand on limestone pavement; locally coarse sand veneer on very coarse sand and grit	N	
HA-12	Houtman Abrolhos	28° 40' 28.71" S, 113° 49' 47.38" E	limestone pavement or mud veneer on coral gravel pavement	N	
HA-13	Houtman Abrolhos	28° 42' 29.35" S, 113° 46' 49.41" E	high wave energy gravelly sand	N	
HA-14	Houtman Abrolhos	28° 44' 32.21" S, 113° 49' 0.27" E	sandy beach with veneer on limestone pavement of coarse and medium sand	N	
HA-15	Houtman Abrolhos	28° 44' 39.98" S, 113° 48' 41.11" E	sandy beach with veneer on limestone pavement of coarse and medium sand	N	
HA-16	Houtman Abrolhos	28° 44' 32.21" S, 113° 49' 0.27" E	sandy beach with veneer on limestone pavement of coarse and medium sand	N	
HA-17	Houtman Abrolhos	28° 44' 50.51" S, 113° 48' 43.35" E	beach of coarse sand	N	
HA-18	Houtman Abrolhos	28° 44' 58.09" S, 113° 48' 27.12" E	beach of coarse sand	N	
HA-19	Houtman Abrolhos	28° 44' 58.55" S, 113° 48' 24.31" E	beach of coarse sand	N	
HA-20	Houtman Abrolhos	28° 53 53.27" S, 114° 00' 22.82" E	limestone gravel pavement	N	
HA-21	Houtman Abrolhos	28° 53' 58.80" S, 114° 00' 19.46" E	sandy beach bordered by limestone gravel to south and rocky shore to north	N	
HA-22	Houtman Abrolhos	28° 54' 21.15" S, 114° 00' 03.60" E	platey limestone pavement	N	
HA-23	Houtman Abrolhos	28° 54' 20.24" S, 114° 00' 00.78" E	platey limestone pavement	N	
HA-24	Houtman Abrolhos	28° 55' 40.22" S, 113° 58' 32.63" E	muddy sand and sand veneer on limestone pavement	N	

Appendix 2

Results of data analyses

Regression analysis of crab abundance and abiotic environmental data from 25 regional transect sites

Least squares bivariate linear regression analyses
Abundance (crabs/m^2) *vs* groundwater Salinity (ppt): $r^2 = 0.0040$, $p = 0.7640$
Abundance (crabs/m^2) *vs* pellicular water salinity (ppt): $r^2 = 0.0124$, $p = 0.\ 0.5967$
Abundance (crabs/m^2) *vs* sediment moisture (% wt): $r^2 = 0.0116$, $p = 0.6082$
Abundance (crabs/m^2) *vs* sediment organic carbon content (% wt): $r^2 = 0.0082$, $p = 0.6672$
Abundance (crabs/m^2) *vs* sediment mud content (% wt): $r^2 = 0.0006$, $p = 0.9046$
Abundance (crabs/m^2) *vs* organic matter in mud (% wt): $r^2 = 0.0050$, $p = 0.7377$

Least squares multiple linear regression
Dependent variable: abundance (crabs/m^2): $r^2 = 0.1546$

MODEL	Coefficients	Standard error	t Stat	*p-value*
Intercept	422.5371	704.6847	0.5996	0.5562
Groundwater salinity (ppt)	- 1.5448	16.4916	- 0.0937	0.9264
Pellicular water salinity (ppt)	- 14.6862	14.0932	- 1.0421	0.3112
Sediment moisture (% wt)	34.3889	23.6608	1.4534	0.1633
Sediment organic carbon content (% wt)	- 135.3204	88.3824	- 1.5311	0.1431
Sediment mud content (% wt)	- 34.1407	47.6225	- 0.7169	0.4826
Organic matter in mud (% wt)	- 7.3094	12.1873	- 0.5998	0.5561

Principal Components Analysis (Varimax and Direct Oblimin Rotations) of the abiotic features of the seven transects of Figure 3.

Rotated Component Matrix[a] (Varimax)		**Component**	
	1	**2**	**3**
Groundwater salinity (ppt)	– 0.116	**0.784**	0.157
Pellicular water salinity (ppt)	**- 0.645**	0.241	**0.428**
Sediment moisture (% wt)	**0.869**	**0.312**	- 0.088
Sediment grain size (μm)	- 0.235	**- 0.763**	0.045
Sediment organic carbon content (% wt)	**0.851**	0.124	0.119
Sediment mud content (% wt)	**0.757**	0.006	**0.343**
Organic matter in mud (% wt)	0.116	**0.592**	**- 0.315**
Depth to water table	**- 0.791**	- 0.057	**0.342**
Crab abundance	– 0.028	0.081	**– 0.790**

Extraction Method: Principal Component Analysis. Rotation Method: Varimax with Kaiser Normalization.
a. Rotation converged in 4 iterations.

Pattern Matrix[a] (Direct Oblimin)		**Component**	
	1	**2**	**3**
Groundwater salinity (ppt)	– 0.143	**0.796**	0.151
Pellicular water salinity (ppt)	**- 0.643**	0.287	**0.388**
Sediment moisture (% wt)	**0.860**	0.263	- 0.033
Sediment grain size (μm)	- 0.204	**- 0.752**	0.030
Sediment organic carbon content (% wt)	**0.858**	0.081	0.174
Sediment mud content (% wt)	**0.777**	- 0.027	**0.392**
Organic matter in mud (% wt)	0.080	**0.580**	**- 0.309**
Depth to water table	**- 0.782**	- 0.006	0.293
Crab abundance	– 0.064	0.065	**– 0.794**

Extraction Method: Principal Component Analysis. Rotation Method: Oblimin with Kaiser Normalization.
a. Rotation converged in 6 iterations.

Results of PRIMER 6		**Component**	
	1	**2**	**3**
Groundwater salinity (ppt)	- 0.038	**0.617**	0.169
Pellicular water salinity (ppt)	**0.337**	**0.313**	**0.324**
Sediment moisture (% wt)	**- 0.506**	0.057	0.040
Sediment grain size (μm)	0.235	**- 0.531**	- 0.025
Sediment organic carbon content (% wt)	**- 0.453**	- 0.084	0.222
Sediment mud content (% wt)	**- 0.368**	- 0.158	**0.424**
Organic matter in mud (% wt)	- 0.170	**0.429**	- 0.241
Depth to water table	**0.449**	0.118	0.215
Crab abundance	- 0.058	0.079	**- 0.729**